ECOLOGY AND STRUCTURE OF FISH COMMUNITIES IN THE

MISSOURI AND LOWER YELLOWSTONE RIVERS

A Dissertation

Presented in Partial Fulfillment of the Requirements for the

Degree of Doctor of Philosophy

with a

Major in Forestry, Wildlife and Range Sciences

in the

College of Graduate Studies

University of Idaho

by

Timothy L. Welker

December 2000

Major Professor: Dennis L. Scarnecchia, Ph.D.

AUTHORIZATION TO SUBMIT DISSERTATION

This dissertation of Timothy L. Welker, submitted for the degree Doctor of Philosophy with a major in Forestry, Wildlife and Range Sciences and titled "Ecology and structure of fish communities in the Missouri and lower Yellowstone Rivers," has been reviewed in final form. Permission, as indicated by the signatures and dates given below, is now granted to submit final copies to the College of Graduate Studies for approval.

Major Professor _____ Date _14 Dec 00_
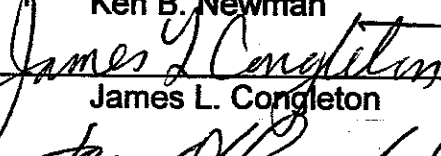Dennis L. Scarnecchia

Committee
Members _____ Date _December 14, 2000_
Ken B. Newman

_____ Date _14 Dec 00_
James L. Congleton

_____ Date _12/19/00_
Jay O'Laughlin
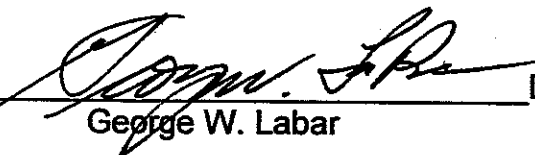
_____ Date _12/14/00_
Kenneth Cain

Department
Administrator _____ Date _12/20/00_
George W. Labar

Discipline's
College Dean _____ Date _12/20/2000_
Charles R. Hatch

Final Approval and Acceptance by the College of Graduate Studies

_____ Date _____
Charles R. Hatch

Preface

Population Structure and Habitat Use of Benthic Fishes along the Missouri and Lower Yellowstone Rivers

This research is reported in 12 volumes. Final Report volumes are listed below and are available from the U. S. Army Corps of Engineers, the primary contracting agency for the overall project. Contact: Becky Latka, U. S. Army Corps of Engineers, CENWO-PM-AE, 106 South 15" Street, Omaha, NE 68102 (rebecca.j.latka@usace.army.mil, 4021221-4602) for copies. Volumes are currently available unless indicated otherwise (anticipated date of publication).

Project Resources. Funding and logistic support were provided by the following agencies and organizations:

Federal - U. S. Army Corps of Engineers, U. S. Bureau of Reclamation, U. S. Environmental Protection Agency, U. S. Fish and Wildlife Service, and U. S. Geological Survey

State Kansas Department of Wildlife and Parks, Iowa Department of Natural Resources, Missouri Department of Conservation, Montana Department of Fish, Wildlife and Parks, North Dakota Game and Fish Department, and South Dakota Department of Game, Fish, and Parks.

University - Kansas State University, Iowa State University, Montana State University, South Dakota State University, University of Idaho, and University of Missouri

Non-government - The Wildlife Management Institute

Final Report: Project Volumes

Berry, C. R. and B. A. Young. 2001. Introduction to the benthic fishes study. Volume 1 of Population structure and habitat use of benthic fishes along the Missouri and lower Yellowstone rivers. U. S. Geological Survey, Cooperative Research Units, South Dakota State University, Box 2140b, Brookings, South Dakota 57007. charles_berry@sdstate.edu

Galat, D. L., M. L. Wildhaber, and D. J. Dieterman. 2001. Spatial patterns of physical habitat. Volume 2 of Population structure and habitat use of benthic fishes along the Missouri and lower Yellowstone rivers. U. S. Geological Survey, Cooperative Research Units, University of Missouri, 302 ABNR Bldg., Columbia, Missouri 65251-7240. galatd@missouri.edu

Berry, C. R., D. L. Galat, and M. L. Wildhaber. 2001. Fish distribution and abundance. Volume 3 of Population structure and habitat use of benthic fishes along the Missouri and Yellowstone rivers. U. S. Geological Survey, Cooperative Research Units, South Dakota State University, Box 2140b, Brookings, South Dakota 57007. charles_berry@sdstate.edu (available August 2001)

Pierce, C. L. C. S. Guy, P. J. Braaten, and M. A. Pegg. 2001. Fish growth, mortality, recruitment, condition, and size structure. Volume 4 of Population structure and habitat use of benthic fishes along the Missouri and lower Yellowstone rivers. U. S. Geological Survey, Cooperative Research Units, Iowa State University, Science Hall II, Ames, Iowa 50011. cpierce@iastate.edu (available August 2001)

Galat, D. L., P. J. Braaten, L. C. Bergstedt, C. R. Berry, D. J. Dieterman, C. S. Guy, M. A. Pegg, C. L. Pierce, M. P. Ruggles, L. C. Sappington, D. Scarnecchia, T. L. Welker, R. G. White, M. L. Wildhaber, and B. A. Young,. 2002. Synthesis. Volume 5 of Population structure and habitat use of benthic fishes along the Missouri and lower Yellowstone Rivers. U. S. Geological Survey, Cooperative Research Units, University of Missouri, 302 ABNR Bldg., Columbia, Missouri 65251-7240. galatd@missouri.edu (available January 2002)

L C. Sappington, M. L. Wildhaber, and D. L. Galat. 2002. Appendices and data. Volume 6 of Population structure and habitat use of benthic fishes along the Missouri and lower Yellowstone rivers. U. S. Geological Survey, Columbia Environmental Research Center, 4200 New Haven Road, Columbia, Missouri 65201. linda_sappington@usgs.gov (available January 2002)

Final Report: Dissertation Volumes

Bergstedt, L. C. 2001. Development of an index of biotic integrity for measuring biological condition on the Missouri River. Ph.D. Dissertation, Montana State University. Volume 7 of Population structure and habitat use of benthic fishes along the Missouri and lower Yellowstone rivers. (available August 2001)

Braaten, P. J. 2000. Growth and mortality of fishes in the Missouri River, with emphasis on freshwater drum. Ph.D. Dissertation, Kansas State University, Manhattan, Kansas. Volume 8 of Population structure and habitat use of benthic fishes along the Missouri and lower Yellowstone rivers.

Dieterman D. J. 2000. Spatial patterns in phenotypes and habitat use of sicklefm chub, *Macrhybopsis meeki,* in the Missouri and lower Yellowstone rivers. Ph.D. Dissertation, University of Missouri, Columbia, Missouri.   Volume 9 of Population structure and habitat use of benthic fishes along the Missouri and lower Yellowstone rivers.

Pegg. 2000, M. A. Hydrological variation along the Missouri River and its effect on the fish community. Ph.D. Dissertation, Iowa State University, Ames, Iowa. Volume 10 of Population structure and habitat use of benthic fishes along the Missouri and lower Yellowstone rivers.

Young. 2001 Intraspecific variation among emerald shiners (*Notropis antherinoides*) of the Missouri River. Ph.D. Dissertation, South Dakota State University, Brookings, South Dakota. Volume 11 of Population structure and habitat use of benthic fishes along the Missouri and lower Yellowstone rivers.

Welker, T. L.   2000. Ecology and structure of fish communities in the Missouri and lower Yellowstone rivers. University of Idaho. Volume 12 of Population structure and habitat use of benthic fishes along the Missouri and lower Yellowstone rivers.

Outreach Product

Berry, C. and D. Galat. 2001. Synopsis of the population structure and habitat use of benthic fishes along the Missouri and Lower Yellowstone rivers. Agriculture Experiment Station Bulletin 7xx, Available from: Bulletin Room, LMHl12, South Dakota State University, Brookings, South Dakota 57007. (available August 2001)

ABSTRACT

In 1995, the Missouri River Benthic Fish Study (MRBFS) was begun with support from the U. S. Army Corps of Engineers, the U. S. Geological Survey, and several state universities. The study was designed to provide information on the status of the benthic-riverine fish communities of the Missouri River from its headwaters in Montana to its mouth at St. Louis, Missouri. The objectives were to: (1) describe habitat use of benthic fishes among dominant benthic macrohabitats within and among study sections and segments; and (2) describe and evaluate recruitment, growth, size structure, body condition, and relative abundance of selected benthic fishes within and among study sections and among segments. Data from the MRBFS and other supplemental data were used to complete this dissertation.

In summers of 1996, 1997, and 1998 fish habitat and fish community data were collected in segments of the Missouri and Yellowstone Rivers and used to examine previously unexplored aspects of the fish community. In the Missouri River in North Dakota, a moderately altered segment and a highly altered segment exhibited greatly different sucker communities. Bigmouth buffalo (*Ictiobus cyprinellus*), smallmouth buffalo (*Ictiobus bubalus*), and river carpsucker (*Carpiodes carpio*) represented 94% of the sucker catch in the moderately altered segment, whereas in the highly altered segment, white sucker (*Catostomus commersonii*) and longnose sucker (*Catostomus catostomus*) constituted 98% of the sucker catch. In the moderately altered segment, high zooplankton densities led to greater sucker zooplanktivory and food niche overlap than in the highly altered segment.

Near the confluence of the Missouri and Yellowstone Rivers the fish community was sampled in four distinct river segments to obtain information on the distribution and habitat use of the flathead chub (*Platygobio gracilis*), sicklefin chub, (*Macrhybopsis meeki*), sturgeon chub (*Macrhybopsis gelida*), and western silvery minnow (*Hybognathus argyritis*), four declining fish species (Family Cyprinidae) native to the Missouri River basin. Catch rates for sicklefin chub and sturgeon chub

were highest in deep main channel habitat and catch rates for flathead chub and western silvery minnow were highest in shallow channel border habitat. Catches of all species were highest in the two segments least altered by anthropogenic disturbance.

The fish communities in a moderately altered segment and two highly altered segments of the Missouri River from the mouth of the Yellowstone River to Kansas City, Missouri were sampled to determine if habitat alterations can influence streamlining and structure of fish communities in altered reaches of a large river. In the least altered segment, higher diversity of depths and current velocities led to a fish community that was less streamlined and that exhibited greater streamlining diversity than in the two highly altered segments, which had lower diversity of depths and velocities.

One lower Yellowstone River segment and three Missouri River segments were sampled to determine if habitat changes caused by a mainstem dam had influenced niche relations among three native cyprinid species–flathead chub, sicklefin chub, and sturgeon chub. Niche relations differed among the three fish species within and among segments. The highest niche overlap among the three species was found in the two segments least altered by anthropogenic disturbance and that exhibited the greatest environmental instability. This result is interpreted to mean that environmental instability and resource partitioning can interact in structuring niche relations among these three cyprinids.

INTRODUCTION

The Missouri River, the longest river in the United States (3,768 km), bisects or borders seven states from its headwaters in Montana to its mouth in Missouri. The highly turbid, productive river (Evermann and Cox 1896) that formerly exhibited frequent flooding and high hydraulic diversity is, as of the 20th century, characterized by reduced sediment transport and a more static hydrograph–a result of dam construction and land use practices throughout the basin. Its channel, once shallow and meandering along most of its length, has been channelized for navigation and its banks stabilized with rock. Only 33% of its length is still unchannelized and free flowing, and 75% of this natural channel is in its headwaters in Montana.

Man-made channel alterations such as mainstem dams, wing dams, and rip-rapped shoreline have led to greater changes in river hydrology and morphology in some sections of the Missouri River than in others. Changes are more pronounced in the lower Missouri River than in stretches of the upper river. Alterations have resulted in changes in fish communities. Some sections of the Missouri River (especially in Montana and western North Dakota) resemble the historical Missouri River with respect to hydrology and morphology, and fish communities have changed little since the turn of the century. Other sections exhibit major changes to both the channel and fish community structure.

Operation of the six mainstem dams by the United States Army Corps of Engineers (USACE) is contingent upon the diversity of needs (navigation, flood control, water supply, irrigation, hydropower, recreation, fish and wildlife) of many individuals and groups. The USACE also is responsible for permitting of dredging and bank stabilization projects. River channel alterations along with pollution and basin land practices have compromised the ecological integrity of the Missouri River hydrosystem.

In 1995, a memorandum of agreement (MOA; No. PD-95-5832) between the Omaha District Corps of Engineers and the National Biological Service (now the United States Geological Survey, Biological Resources Division) was established to provide the USACE and state and federal aquatic resource agencies with the

necessary information for compliance with the Endangered Species Act. Under the agreement, six USGS research stations and their parent universities (Montana State University, University of Idaho, South Dakota State University, Iowa State University, Kansas State University, University of Missouri - Columbia) and a state natural resource agency (Montana Department of Fish, Wildlife, and Parks) collectively known as the Missouri River Benthic Fishes Consortium (MRBFC) collected information on the benthic fish community and their habitats in sections and segments throughout the river from Montana to Missouri. The study is known as the Missouri River Benthic Fish Study (MRBFS).

A list of target benthic fish from which information would be collected was developed by the MRBFC on the basis of commercial importance (e.g., bigmouth buffalo, *Ictiobus cyprinellus*; smallmouth buffalo, *Ictiobus bubalus*; channel catfish, *Ictalurus punctatus*), endangered or threatened status (e.g., pallid sturgeon, *Scaphirhynchus albus*; sturgeon chub, *Macrhybopsis gelida*; sicklefin chub, *Macrhybopsis meeki*) or recreational importance (e.g., blue catfish, *Ictalurus furcatus*; walleye, *Stizostedion vitreum*; sauger, *Stizostedion canadense*). To insure that fish and habitat data were collected in a uniform manner in each river section, the MRBFC standardized sampling by developing and using a set of standard operating procedures. The MRBFC formulated two research objectives which were met by the MRBFS: (1) Describe habitat use of benthic fishes among dominant benthic macrohabitats within and among study sections and segments; and (2) Describe and evaluate recruitment, growth, size structure, body condition, and relative abundance of selected benthic fishes within and among study sections and among segments. The MRBFS also supported six Ph. D. dissertations. The dissertations provided additional information that was also used to answer the two research objectives.

The University of Idaho, through the Idaho Cooperative Fish and Wildlife Research Unit, was responsible for sampling MRBFS segments 10 and 12 of the Missouri River, both located within the state boundaries of North Dakota (Figure 1.1). A large data set containing information on the population structure and habitat use of benthic fish was compiled at the completion of the MRBFS. Data from this

large data set as well as additional collected data were used to complete this dissertation.

Four objectives are addressed in this dissertation that examine previously unexplored aspects of the fish communities in segments of the Missouri River. These objectives were to: 1) examine the distribution, abundance, and feeding ecology of Catostomid fishes in the Missouri River, North Dakota (Chapter 2); 2) examine habitat use and population and community structure of native fishes in the upper Missouri and lower Yellowstone Rivers, North Dakota (Chapter 3); 3) examine the relationship among habitat alterations, fish ecomorphology, and fish community structure in the Missouri River system (Chapter 4); and 4) examine habitat use and habitat niche relations for three native Cyprinids in the Missouri River hydrosystem (Chapter 5).

ACKNOWLEDGMENTS

TABLE OF CONTENTS

Page

CHAPTER THREE. Habitat use and population and community structure of native fishes in the upper Missouri and lower Yellowstone Rivers, North Dakota.

CHAPTER FOUR. Habitat alterations, fish ecomorphology, and fish community structure in the Missouri River system.

CHAPTER FIVE. Habitat use and habitat niche relations for three native cyprinids in the Missouri River hydrosystem.

LIST OF FIGURES

Figure   Page

Figure   Page

Figure   Page

Figure   Page

LIST OF TABLES

Table   Page

Table   Page

Table   Page

CHAPTER 1

Overview of the Missouri River Hydrosystem

The Missouri River is the longest river in the United States, stretching 3,768 km from Three Forks, Montana where the Madison, Jefferson, and Gallatin Rivers join to form its headwaters to its mouth where it joins the Mississippi River near St. Louis, Missouri (Figure 1.1). The river basin encompasses 137 million ha (Figure 1.1) and the topography varies from 14.5 million ha of Rocky Mountains in the west, to 95.8 million ha of the Great Plains further east, to 23.3 million ha of Central Lowlands in the lower basin (Hesse et al. 1989).

Geology

The topography to the south and west of the Missouri River has been shaped by erosion of a fluvial plain extending eastward from the Rocky Mountains. The topography north and east of the Missouri River has been shaped by erosion of the glacial drift and till from continental glaciation. The river once flowed north into Hudson Bay until glacial events during the Pleistocene glaciation turned it southward. These geological features have led to a unique drainage pattern in the upper and lower Missouri River basin; every major tributary except the Milk and James Rivers is a right bank tributary that flows to the east or the northeast. In the basin below the mouth of the Kansas River, a greater number of left bank tributaries exists (U. S. Army Corps of Engineers 1985). In the upper Missouri River basin, the valley is only 240 m wide and the river is a clear mountain stream running through mountainous terrain. In the lower basin, before mainstem alteration, the river varied from 2.4 to 27.4 km in width, averaging 8.1 km and traversed through alternating prairie and deciduous forest (Hesse et al. 1989).

Mainstem River Physical Characteristics and Alterations

Prior to intense anthropogenic disturbance within the Missouri River basin, the Missouri River was heavily laden with silt. In 1944, the Missouri River

transported 228.6 million tons of sediment downstream (Slizeski et al. 1982). The Missouri River was also characterized by two general periods of flooding, a "March rise" and a "June rise". The "March rise" resulted from snow melt in the plains and the "June rise" was caused by runoff from melting mountain snow in the upper basin and rainfall throughout the basin.

Humans have been altering the Missouri River channel since the first explorers and fur traders removed snags and tree tops to improve boat passage (Hart 1957, Funk and Robinson 1974). Channel alterations have been a Federal government activity since 1884, first by the Missouri River Commission and, since 1902, by the U. S. Army Corps of Engineers (USACE). In response to the need for a dependable water supply for irrigation, navigation, and mining, development of the Missouri River basin's water resources culminated with the Pick-Sloan Plan (adopted in 1944) (Hesse et al. 1989). The Pick-Sloan Plan included a comprehensive plan of development for the entire Missouri River Basin, including irrigation, navigation, hydropower, flood control, water quality, water supply, fish, wildlife, and recreation. The backbone of this plan was the construction of six mainstem dams and reservoirs on the upper and middle reaches of the Missouri River, which began in the 1930's and ended in the 1960's.

Development of the lower Missouri River for commercial navigation and flood control was initiated by the Missouri River Bank Stabilization and Navigation Project which was completed in 1981. Through this project, the lower Missouri River from Ponca, Nebraska to the confluence with the Mississippi River was transformed into a much narrower and deeper channel for navigation. Channel dimensions (2.7 m deep by 91.4 m wide) are maintained with dikes, revetments, and sills (Slizeski et al. 1982). The channel nearly maintains itself through scouring. The natural river's "offset V" shape has been altered to a trapezoidal shape. The change in channel shape has reduced the diversity of depths and velocities in the river (Hesse and Sheets 1993).

The impoundment of nearly one-third of the Missouri River has reduced sediment and organic matter transport, and modified flows along much of the river's

length (Dryer and Sandvol 1993). These activities have altered the natural flow regimes, turbidity, nutrient levels, and channel dynamics resulting in destruction and alteration of aquatic habitats. An additional one-third of the Missouri River between Sioux City, Iowa and St. Louis, Missouri has been channelized. Channelization has resulted in reduced abundance of many main channel and off-channel habitats and has altered channel hydrodynamics. Only one-third of the Missouri River remains free-flowing and most of that is in Montana.

The natural flow regime has been disrupted and modified greatly by six mainstem dams. Today, dams reduce flows from April to July (the period of natural rise) for flood control and increase them from July to April (the period of natural decline).

Each reservoir also acts as a sediment trap. By 1954 the annual silt load of the Missouri River had been reduced by 81% (Hesse et al. 1989). The reduction in sediment transport from upstream reaches has led to unnatural aggredation and degradation processes. The water leaving mainstem dams is sediment poor and therefore degrades the channel bed reducing substrate diversity and deepening the channel (Berkas 1995). The disruption in the continual sediment removal and deposition processes has altered the natural channel and habitat dynamics in the middle and lower Missouri River, changing it from a braided channel with sandbars and eroding banks into a deeper and narrower rock-lined main channel devoid of many natural aquatic habitats, such as backwaters and side channels (Hesse and Sheets 1987).

In addition to trapping sediment, mainstem reservoirs trap organic material, preventing transport downstream. Clear, sediment poor water leaving the dams seeks a load to carry, causing deepening of the channel bed which severs backwater connections with the mainstem river and eliminates or reduces river-floodplain connectivity (Hesse 1987). Bank stabilization structures, such as rip-rap and wingdams, in many below dam reaches of Missouri River prevent natural river meandering. Allochthonous carbon inputs to below dam sections of river undoubtedly have been reduced by these mainstem alterations, as well as by

reduced floodplain forest productivity.

Changes in other aspects of channel dynamics have had ecological effects. Early stages of ecological succession have been reduced as new habitats are lost in the Missouri River. Since 1826, mature forest composition has not changed considerably (Bragg and Tatschl 1977), however, the proportion of mature forests to other successional stages is increasing (Hesse et al. 1988). Forest productivity has been linked to forest age (Molles, Jr. 1998), where younger forests produce more organic material which is an important energy source for heterotrophic rivers and streams (Allan 1995).

Productivity of remaining forest lands in the Missouri River floodplain has declined because of the loss of a periodic river-floodplain connection and conversion of much of the riparian zone into agriculture fields. Reiley and Johnson (1982) examined tree core data for the major tree species in the North Dakota floodplain below Garrison Dam and found post-dam tree growth had declined when compared to the pre-dam period. This decline in productivity is related to a reduction in over bank flooding which has led to the absence of an annual soil profile saturation (Reiley and Johnson 1982) and a lack of silt and nutrient deposition (Burgess et al. 1973). A lower water table in spring designed to reduce downstream flooding at a time when floodplain trees have a high water demand has also reduced floodplain forest productivity (Reiley and Johnson 1982). Decreased forest productivity, reduced river meandering, and an absence of overbank flooding has led to a decline in the amount of organic matter produced and decreased its availability to aquatic organisms in below-dam reaches of the Missouri River.

Conversion of the lower Missouri River into a narrow navigation channel has led to decreased channel length and width. For example, the distance from Rulo, Nebraska to the mouth near St. Louis, Missouri was 875.5 km in 1879. By 1972, the distance had been reduced to 802.1 km (Funk and Robinson 1974). In this stretch of river, there has been a loss of 73.4 km of river over this 93 year period which is over eight percent of the length. An average km of lower Missouri River in 1954 had a surface area of 89.8 ha which has resulted in a loss of over 1,600 ha in the stretch

of river from Rulo to the mouth (Funk and Robinson 1974). Additionally, the total water surface area in the Missouri River in 1879 was 49,266 ha. By 1954, it had been reduced to 28,794 ha; a loss of 20,472 ha. This loss was due to channel narrowing through dike construction and the cutting off of meanders (Funk and Robinson 1974). The loss of river surface area implies the loss in river habitat for many aquatic organisms.

Dike, wingdam, and rip-rap construction have also led to other habitat alterations. Unconnected islands were almost eliminated from the Missouri River between 1879 and 1954. The surface area of islands was reduced from 9,882 ha to 169.6 ha, a loss of ninety-eight percent; the number of islands was reduced from 161 in 1879 to 18 in 1954 (Funk and Robinson 1974). Many secondary channels, backwaters, and sand bars were also eliminated in this portion of the Missouri River. These habitats were characterized by shallower depths and slower current velocities than the main channel and were important rearing, feeding, and refuge areas for many fish species.

Fish

Discharge fluctuations during the spring months have the greatest deleterious affects on spawning of native fish. Below Fort Randall dam in South Dakota, Hesse and Mestl (1985) showed a relationship between modified spring flows and poor year class strength of native fishes such as river carpsucker (*Carpiodes carpio*), smallmouth buffalo (*Ictiobus bubalus*), bigmouth buffalo (*Ictiobus cyprinellus*), shorthead redhorse (*Moxostoma macrolepidotum*), channel catfish (*Ictalurus punctatus*), flathead catfish (*Pylodictis olivaris*), sauger (*Stizostedion canadense*), and common carp (*Cyprinus carpio*). Also, the interaction of reduced flows, a deeper channel, and bank stabilization has disrupted the natural flood plain - river complex dynamics and reduced habitat for fish (Hesse and Sheets 1993). Native fish use various habitats in natural river for reproduction, feeding, cover, and refuge. This loss of habitat has drastically reduced numbers of many native fish species such as the pallid sturgeon (*Scaphirhynchus albus*) (Dryer and Sandvol 1993), sicklefin chub (*Macrhybopsis meeki*), sturgeon chub (*Macrhybopsis gelida*), flathead

chub (*Platygobio gracilis*), blue sucker (*Cycleptus elongatus*), and paddlefish (*Polyodon spathula*) (Werdon 1993).

The negative effects of habitat degradation on native fishes from the lower Missouri River can be seen in commercial harvest. In Missouri, the commercial catch declined steadily from 671,215 kg in 1945 to a low of 70,768 kg in 1965, a decline of more than eighty percent (Hesse et al. 1989). This decline in commercial catch is attributable to reduced habitat diversity and lower fish biomass.

Man-made channel alterations such as mainstem dams, wing dams, and rip-rapped shoreline have led to greater changes in river hydrology and morphology in some sections of the Missouri River (e.g. lower sections) than in others (some upper sections). Fish communities have been correspondingly affected. Some sections of the Missouri River (especially in Montana and western North Dakota) closely resemble the historical Missouri River with respect to hydrology and morphology, and fish communities have changed little since the turn of the century. Other sections, such as those below dams or in the lower channelized river, exhibit major channel changes and major changes in fish community structure. To help maintain the remaining native species, information is needed on the habitat factors associated with stable and declining native fish populations in the river.

LITERATURE CITED

Allan, J. D. 1995. Stream ecology: structure and function of running waters. Chapman--Hall, London.

Berkas, W. R. 1995. Transport and sources of sediment in the Missouri River between Garrison Dam and the headwaters of Lake Oahe, North Dakota, May 1988 through April 1991. Water-resources investigations report 95-4087. U. S. Department of the Interior, U. S. Geological Survey, Bismarck, North Dakota.

Bragg, T. B., and A. K. Tatschl. 1977. Changes in floodplain vegetation and land use along the Missouri River from 1826 to 1972. Environmental Management

1:343-348.

Burgess, R. I., W. C. Johnson, and W. R. Keammerer. 1973. Vegetation of the Missouri River floodplain in North Dakota. Report WI-221-018-73. North Dakota Water Resources Research Institute, North Dakota State University, Fargo.

Dryer, M. P., and A. J. Sandvol. 1993. Recovery plan for the pallid sturgeon (*Scaphirhynchus albus*). U. S. Department of the Interior, U. S. Fish and Wildlife Service, Ecological Services, Bismarck, North Dakota.

Funk, J. L., and J. W. Robinson. 1974. Changes in the channel of the lower Missouri River and effects on fish and wildlife. Missouri Department of Conservation, Aquatic Series No. 11, Jefferson City.

Hart, H. 1957. The dark Missouri. University of Wisconsin Press, Madison.

Hesse, L. W., and G. Mestl. 1985. Ecology of unchannelized reaches of the Missouri River. Dingle-Johnson Project Number F-75-R, Progress Report. Nebraska Game and Parks Commission, Norfolk, Nebraska.

Hesse, L. W. 1987. Taming the wild Missouri River: what has it cost? Fisheries 12(2): 2-9.

Hesse, L. W., and C. W. Wolfe, and N. K. Cole. 1988. Some aspects of energy flow in the Missouri River ecosystem and a rationale for recovery. Pages 13-29 *in* N. G. Benson, editor. The Missouri River- the resources, their uses, and values. North Central Division American Fisheries Society, Special Publication 8, Bethesda, Maryland.

Hesse, L. W., J. C. Schmulbach, J. M. Carr, K. D. Keenlyne, D. G. Unkenholz, J. W. Robinson, and G. E. Mestl. 1989. Missouri River fishery resources in relation to past, present, and future stresses. Pages 352-371 *in* D. P. Dodge, editor. Proceedings of the International Large River Symposium. Canadian Special Publications of Fisheries and Aquatic Science, 106, Ottawa, Ontario, Canada.

Hesse, L. W., and G. E. Mestl. 1993. An alternative hydrograph for the Missouri River based on the precontrol condition. North American Journal of Fisheries Management 13: 360-366.

Hesse, L. W., and W. Sheets. 1993. The Missouri River hydrosystem. Fisheries 18(5): 5-14.

Molles Jr., M.C., C. S. Crawford, L. M. Ellis, H. M. Valett, and C. N. Dahm. 1998. Managed flooding for riparian ecosystem restoration. Bioscience 48:749-756.

Reiley, P. W., and W. C. Johnson. 1982. The effects of altered hydrologic regime on tree growth along the Missouri River in North Dakota. Canadian Journal of Botany 60:2410-2423.

Slizeski, J. J., J. L. Andersen, and W. G. Dorough. 1982. Hydrologic setting, system operation, present and future stresses. Pages 15-37 *in* L. W. Hesse et al., editors. The Middle Missouri River. The Missouri River Study Group, Norfolk, Nebraska.

U. S. Army Corps of Engineers. 1985. Missouri River mainstem reservoirs. Summary of actual 1984-1985 operations and operating plan for 1985-1986. Omaha, Nebraska.

Werdon, S. J. 1993. Status report on sicklefin chub (*Macrhybopsis meeki*), a candidate endangered species. U. S. Department of Interior, U. S. Fish and Wildlife Service, Ecological Services, Bismarck, North Dakota.

CHAPTER 2

Distribution, Abundance, and Feeding Ecology of Catostomid Fishes in the Missouri River, North Dakota

ABSTRACT

In 1997 and 1998, sampling was conducted on the Missouri River, North Dakota to determine if human caused disturbances had influenced Catostomid species composition and feeding ecology. The study area consisted of two distinct river segments, the Missouri River between the mouth of the Yellowstone River and Lake Sakakawea (the Yellowstone-Sakakawea segment), a moderately altered segment and the Missouri River between Garrison Dam and Lake Oahe (the Garrison-Oahe segment), a highly altered segment. The segments exhibited greatly different sucker communities. Bigmouth buffalo (*Ictiobus cyprinellus*), smallmouth buffalo (*Ictiobus bubalus*), and river carpsucker (*Carpiodes carpio*) represented 94% of the sucker catch in the Yellowstone-Sakakawea segment, whereas in the Garrison-Oahe segment, white sucker (*Catostomus commersonii*) and longnose sucker (*Catostomus catostomus*) constituted 98% of the sucker catch. In the Yellowstone-Sakakawea segment, high zooplankton densities led to greater sucker zooplanktivory and food niche overlap than in the Garrison-Oahe segment. Intense anthropogenic disturbances to the Garrison-Oahe segment are associated with the differences in sucker species composition, prey density and composition, and sucker food habits and food niche overlap between the two segments. Restoring natural river conditions, such as a high sediment load, channel meandering, and a periodic flood pulse, that maintain natural prey populations and a diversity of natural habitats is critical for the survival of native sucker species in the Garrison-Oahe segment and other altered Missouri River segments.

INTRODUCTION

Catostomid fishes include about 70 species of relatively large, chiefly North American fishes commonly known as suckers (Helfman et al. 1997). These Cypriniform fishes are predominately bottom dwelling and possess specialized lips and premaxillaries which allow them to feed effectively on bottom organisms. Suckers generally inhabit unpolluted waters and can be found living under a variety of riverine and lake conditions, but most species generally cannot tolerate extensive modification of their habitats (Smith 1979).

Impoundment of rivers has frequently led to changes in native fish ecology and abundance in rivers below dams (Miller 1959, Anderson et al. 1983, Martinez et al. 1994, Cambray et al. 1997). Declines in the abundance of native species following river regulation have been documented in many large, turbid rivers, such as the Colorado (Minckley 1991, Schmidt et al. 1998) and the Missouri (Funk and Robinson 1974, Hesse et al. 1989, Galat 1998). Changes in river characteristics such as water temperature, flooding, peak flows, and substrate composition have been implicated as causes of native fish decline and the concomitant increase in non-native species.

Development of the Missouri River basin's water resources began in the 1800's in response to the need for a dependable water supply for irrigation, navigation, and mining, culminating with the Pick-Sloan Plan (adopted in 1944) (Hesse et al. 1989). The Pick-Sloan Plan included a comprehensive plan of development for the entire Missouri River Basin, including irrigation, navigation, hydropower, flood control, water quality, water supply, fish, wildlife, and recreation. The backbone of this plan was the construction of six mainstem dams and reservoirs on the upper and middle reaches of the Missouri River, which began in the 1930's and ended in the 1960's. These dams have changed the water quality and fish habitat in the river which has led to changes in fish community composition. In the Missouri River, declines of many native fish have been attributed to dam

construction and other man-induced changes resulting from implementation of the Pick-Sloan Plan (Hesse et al. 1989).

The Missouri River supports a diverse assemblage of species within the family Catostomidae. There is evidence, however, that many of these species have declined in abundance since dam construction and channelization began on the river (Funk and Robinson 1974). Although many of these fish are important commercial, recreational, and forages species and have been studied in impoundments and smaller rivers, the status and ecology of most of these sucker species in the Missouri River is not well known.

Detailed knowledge of the food habits of a fish community can give valuable insight into interspecific interactions, niche dimensions, food resource partitioning, and the trophic status of individual species (Litvak and Hansell 1990, Gray et al. 1997). Discovering and understanding these components of feeding ecology is key to proper management and conservation of fish species. Yet, despite the abundance and widespread distribution of sucker species in the Missouri River, the feeding ecology of these fish has received little attention. Food habits of species in the Genus *Ictiobus* have been described for one Missouri River reservoir (Lewis and Clark Lake) (McComish 1967), but riverine food habits and the feeding ecology of these and other Missouri River suckers are unknown.

Understanding how man-induced impacts to the river have influenced sucker distribution, abundance, and ecology is an important first step in identifying conservation and restoration measures. The objectives of this study were to: 1) contrast sucker community composition during summer in two riverine upper Missouri River segments in North Dakota, one exhibiting pre-impoundment physical and biological characteristics and the other heavily modified by humans; 2) determine if anthropogenic disturbances influence aspects of sucker feeding ecology (food habits, feeding strategy, and food niche overlap) in these same river segments.

STUDY AREA

North Dakota contains two inter-reservoir segments of the Missouri River within its state boundaries. One segment extends from the Yellowstone-Missouri River confluence (Missouri River km (rkm) 2546.0) near the North Dakota-Montana border to its lower boundary of Lake Sakakawea (rkm 2470.3) and hereafter is referred to as the Yellowstone-Sakakawea segment or YSS (Figure 2.1). The second segment extends from Garrison Dam (rkm 2235.4) in south-central North Dakota to its lower boundary of Lake Oahe (rkm 2051.9) near the North Dakota-South Dakota border and hereafter is referred to as the Garrison-Oahe segment or GOS (Figure 2.1).

The two segments are characterized by different habitat characteristics and flow regimes. The YSS is free-flowing with a semi-natural hydrograph, a result of the merging of the free-flowing Yellowstone River and the Missouri River which is regulated upriver by Fort Peck Dam. This segment is characterized by high main channel turbidity, no major shoreline development, and few revetment banks (rip-rap). The lack of shoreline development and revetment banks allows the main river channel to meander naturally which creates a diversity of off-channel habitats. The GOS, in contrast, exhibits fewer pre-impoundment physical and biological characteristics. Garrison Dam and Lake Sakakawea have created an alluvium sink, thereby reducing the sediment load in the river below the dam (Berkas 1995). The river below the dam is uncharacteristically clear and natural aggradative and degradative processes have been disrupted. Furthermore, the dam regulates the hydrograph and hypolimnetic withdrawals from Lake Sakakawea have created uncharacteristically cool water temperatures during the summer with maximum summer temperatures approximately 9 °C cooler than before impoundment (Everett 1999). This segment is also characterized by numerous revetments and a much higher degree of shoreline development and bank stabilization (25-40%) than the YSS.

METHODS

Data Collection

Sucker Data Collection

A stratified random sample was used to collect suckers in both the YSS and the GOS where the strata were macrohabitat types. These macrohabitats were main channel cross-over, outside bend, inside bend, secondary channel: non-connected, secondary channel: connected, tributary mouth (Figure 2.2). In both segments, macrohabitats served as sampling units. Suckers were collected from five randomly selected sampling units of each macrohabitat type in each segment from June through August in both 1997 and 1998. A variety of fish capturing gears was used that would sample a wide variety of sucker species and sizes, thereby ensuring accurate description of the sucker community in each segment. These gears were a bag seine (10.7 m long, 1.8 m high, 1.8 m^3 bag, 5 mm mesh), a benthic beam trawl (2 m wide, 0.5 m high, 5.5 m long, 3.2 mm inner bag mesh), a trammel net (22.9 m long, inner wall 2.4 m deep with 2.5 cm mesh, outer wall 1.8 m deep with 20.3 cm mesh), an electrofishing boat (Coffelt VVP-15 variable voltage pulsator, 5,000 W generator), a gill net (30.5 m long, 1.8 m high, mesh sizes of 1.9 cm, 3.8 cm, 5.1 cm, 7.6 cm), and a hoop net (4.8 m in length, 3.7 cm diameter mesh, finger style throat, seven fiberglass hoops, and a 15.2 m lead attached to the first hoop made of 3.8 cm mesh). A subsample was a single gear sample.

Benthic and Pelagic Invertebrate Data Collection

Benthic macroinvertebrates and pelagic micro- and macroinvertebrates were collected at each fish collection subsample to provide food selectivity information for each species of sucker. Benthic macroinvertebrates were collected with a Ponar dredge (22.9 cm x 22.9 cm). Three ponar grabs were taken at each gear subsample location, combined, and placed into a wash bucket that contained a 541 μm sieve screen bottom. The sample was washed and the remaining sediment, debris, and macroinvertebrates placed into a container and preserved with 95% ethanol for lab transport and analysis. In the lab, benthic invertebrates were

identified to family if possible. Invertebrate density was expressed as number of organisms/m².

Pelagic invertebrates were collected with a Wisconsin plankton net (10.8 cm diameter, 80 μm mesh) fitted with a General Oceanics flow meter. A single tow was taken to survey pelagic invertebrates at each gear subsample. For subsamples with high current velocities (>0.2 m/s), the boat was anchored and the plankton net was attached to a hangar bar and 22.7 kg sounding weight and lowered to 0.8 of the total depth with an A55M sounding reel. The net remained suspended at this depth for 3 min.

For low current velocity subsamples (<0.2 m/s) the plankton net was attached to a 2 m standard wading rod at the 0.8 total depth mark and deployed for 3 min near the center of the area sampled. In macrohabitats with near zero current velocities, the net was towed by hand or boat for 3 min.

All material was removed from the plankton net and preserved in 95% ethanol. In the lab, pelagic invertebrates were identified in most cases to family. The volume of water sampled by the net was determined using the flow meter. Invertebrate density was expressed as number of organisms/liter.

Sampling of Sucker Digestive Tracts

Only fish that were large enough to have reached sexual maturity (adult fish) were sampled for food habits analysis. Sexual maturity for each species was determined using lengths provided by Trautman (1957) and Scott and Crossman (1973). Contents were removed from the anterior one-fifth of the digestive tract of each sucker, up to the first bend and preserved in 15% formalin solution. After fixation, the contents were transferred to 95% ethanol until examined.

To quantify prey eaten by suckers, foregut contents of individual fish were diluted in 50 –1,000 ml of water and suspended with a magnetic stir bar. Three separate two ml subsamples were taken with a plunger-type subsampler and placed in a counting chamber. If a stomach could not be effectively subsampled, the entire contents were analyzed. All invertebrates in each subsample were enumerated using a dissecting scope and identified to family whenever possible. Relative

importance of food categories was determined by counting the number of intersections on an ocular grid that were covered by individuals of each food category (Minckley et al. 1970). For partially digested aquatic insect larvae, such as Chironomidae, surface area was determined using regression equations derived from a regression of surface area on head capsule width (Hyslop 1980). All other food items were measured with the ocular grid and missing portions estimated visually.

Because the importance of food categories could be overestimated or underestimated using a surface area technique, a weight estimate was also used to provide a more accurate estimate of food category importance. To determine if surface area and weight estimates differed, surface area and weight proportional importance were determined for stomach contents taken from twenty-five smallmouth buffalo (*Ictiobus bubalus*). Weights of food items were either measured with an analytical balance or estimated with published regression equations (Dumont et al. 1975, Smock 1980). A randomized block analysis of variance (ANOVA) was used to test for differences between relative importance values of food categories derived from surface area measurements and those derived from weight measurements. Type of estimate served as treatments and type of invertebrate (zooplankton and benthic macroinvertebrate) served as the blocking variable. Relative importance values obtained from the two methods did not differ significantly (P=0.32) and therefore, the less time consuming surface area method was used to determine food category importance.

Statistical Analysis

Quantifying Species Richness and Diversity of Prey Populations

The species richness and diversity of zooplankton and benthic invertebrate prey populations in sucker habitats were quantified. Species richness was determined by counting the number of each prey category in a sample and then averaging across all samples in a macrohabitat sample unit. Richness values obtained in macrohabitat sample units were then averaged to get the segment

average. Prey diversity was quantified with the reciprocal of Simpson's index D (Hill 1973).

(2.1) $D = \sum p_i^2$ (i=1,.....,s prey categories)

where D is Simpson's index, p_i is the proportion of prey category i in the community, and $\sum p_i = 1.0$.

Prey diversity was quantified with the equation:

(2.2) $1/D$ = prey diversity

where 1/D is the reciprocal of equation 2.1 which varies from 1 to s, the number of prey categories in the sample. The diversity of prey types was determined at each subsample within a macrohabitat sample unit. The subsample diversities were then averaged to obtain the prey diversity within the sample unit.

ANOVA was used to test the following null hypotheses: 1) there was no difference in zooplankton densities between the YOS and the GOS habitats (i.e., $Ho=\mu_1=\mu_2$), 2) there was no difference in benthic invertebrate densities between the YOS and the GOS habitats, 3) there was no difference in zooplankton richness between the YOS and the GOS habitats, 4) there was no difference in benthic invertebrate richness between the YOS and the GOS habitats, 5) there was no difference in zooplankton diversities between the YOS and the GOS habitats, and 6) there was no difference in benthic invertebrate diversities between the YOS and the GOS habitats. Segments served as treatments (YOS and GOS) and years (1997 and 1998) served as blocks. Zooplankton and benthic invertebrate density, richness, and diversity served as dependent variables. Prey density, richness, and diversity values were log (y+1) transformed to handle non-normality.

Feeding Ecology and Food Habits

Food Habits

Food habits were quantified with several indices. The percent surface area (%A) of each food category was determined for each fish species. In addition, the percent of occurrence (%F), and percent number (%N) were determined for each category for each species of sucker. The equations used were:

(2.3)   %A = (Q_i /Q_t) X 100, $Q_t = \sum_{(i=1)} n^* Q_i$

(2.4) %N = (B_i / B_t) X 100, $B_t = \sum_{(i=1)} B_i$

(2.5) %F = (O_i / O_t) X 100, $O_t = \sum_{(i=1)} O_i$

where Q_i is the surface area composed by prey i, Q_t is the total surface area of all digestive tract items in the entire digestive tract sample, n is the number of individual prey of a prey type in the digestive tract sample, B_i is the digestive tract content number composed by prey i, B_t is the total digestive tract content number of all digestive contents in the entire sample, O_i is the number of suckers with prey i in their digestive tract, and O_t is the total number of suckers with digestive tract contents.

Linear least-squares regression was used to test the null hypothesis that there was no relationship between prey density and relative abundance of prey in sucker stomachs. The relative abundance of prey was determined for each sucker and compared with regression analysis against prey density at each capture site. Prey relative abundance served as the response (Y) variable and prey density served as the predictor (X) variable.

(2.6) $y = \beta_0 + \beta_1 x$

where y = prey relative abundance in a fish stomach, β_0 = y-intercept, β_1 = slope, and x = prey density in the environment (benthic invertebrates = number/m^2 or zooplankton = number/liter).

This analysis was conducted separately for zooplankton (Cladocera and Copepoda) and Chironomid larvae in both the YSS and the GOS and used to test the H_o : $\beta_1 = 0$, i.e., there is no linear relationship between prey relative abundance in sucker stomachs and prey density at capture sites. Prey relative abundance values were arcsine (square root (y)) transformed to handle possible non-normality.

Electivity

The feeding habits of fish and the availability of food resources were compared using Strauss' linear food selection index L.

(2.7) $L_i = r_i - p_i$

where r_i is the proportion (percent number) of a given prey type A (food category) in the predator's diet and p_i is the fraction (percent number) of the same prey A in the

environment (Strauss 1979). Food selection values derived from equation 2.7 for each food category were averaged for each sucker species in a segment.

Feeding Strategy and Food Resource Niche Breadth and Overlap

A modification of the graphical Costello method (Amundsen et al. 1996) also was used to analyze stomach contents data. Prey-specific abundance was plotted against frequency of occurrence on a two-dimensional graph (Figure 2.3). Prey-specific abundance is the percentage a prey taxon comprises of all prey items in only those predators with prey i in their stomach:

(2.8) $P_i = (\Sigma S_i / \Sigma S_{ti}) \times 100$

where P_i is the prey-specific abundance of prey i, S_i the stomach content (surface area) comprised by prey i, and S_{ti} the total stomach content in only those suckers with prey i in their stomach.

Information about feeding strategy and prey importance of the population can be obtained by examination of distributions of points along the diagonals and axes of the diagram depicted in Figure 2.3. The percent abundance, increasing along the diagonal from the lower left to the upper right corner, provides a measure of prey importance, with dominant prey at the upper right, and rare or unimportant prey at the lower left. The vertical axis represents the feeding strategy of the predator in terms of specialization or generalization (Figure 2.3). The predators have specialized on prey types in the upper part of the figure, whereas prey located in the lower portion were eaten more occasionally. Prey points located at the upper left of the diagram would be indicative of specialization of the predator population. This graphical method allows the exploration and graphical representation of prey importance, feeding strategy, and the inter- and intra-individual components of niche width.

For each sucker species, niche breadth (B) for food items was calculated using the equation of Levins (1968):

(2.9) $B = 1/\Sigma P_i^2$ (i=1,....,n prey types),

and then standardized to express it on a scale from 0 to 1.0:

(2.10) $B_A = (B-1) / (n-1)$

where P_i is the proportion of the resource in each category and n is the number of types of prey items. Equation *2.10* was used to assess the diversity of food items eaten by each Catostomid species in a segment.

For these same food items, niche overlap (R_o) between each pair of sucker species was determined using Horn's (1966) equation:

(2.11) $R_o = (\Sigma(p_{ij} + p_{ik})\log(p_{ij} + p_{ik}) - \Sigma p_{ij} \log p_{ij} - \Sigma p_{ik} \log p_{ik}) / 2 \log 2$,

(i = 1,.....,n prey types; j = 1,....., n sucker species)

where p_{ij} is the proportion that prey type i is of the total prey used by species j, p_{ik} is the proportion that prey type i is of the total prey used by species k.

The values for equation *2.11* range from 0 to 1, with 1 indicating complete overlap, 0.33 or less indicating low overlap, and 0.66 or greater indicating high overlap. Diet similarities between species pairs were assessed with *(2.11)*.

The null hypothesis that there was no relationship between sucker food niche breadth (B_A, equation *2.10*) and prey species diversity (1/D, equation *2.2*) ($H_o = \beta_1 = 0$, i.e., there is no linear relationship between sucker food niche breadth and prey species diversity at capture sites) was tested with regression analysis in the GOS and the YSS. Food niche breadth served as the response (Y) variable and prey species diversity served as the predictor (X) variable.

(2.12) $y = \beta_0 + \beta_1 x$

where y = food niche breadth (B_A), β_0 = y-intercept, β_1 = slope, and x = prey species diversity (1/D).

This analysis was conducted separately for zooplankton and benthic invertebrate prey.

Distinctiveness of the food niche within the family Catostomidae was assessed in part with a multivariate technique. The null hypothesis that there was no difference in food resource use among sucker species was tested using multivariate analysis of variance (MANOVA; Johnson and Wichern 1992) conducted across species in each river segment, with sucker species as the independent variable and food categories as the dependent variable (percent surface area importance values) (Johnson and Wichern 1992). The equal variance-covariance

assumption was checked with the Box test (Box 1949) and residual plots for dependent variables were constructed to examine homoscedasticity. Multicollinearity between dependent variables was examined by computing the variance inflation factor. Dependent variables (% surface area values) were arcsine (square root (y)) transformed.

The MANOVA is used to assess food habit use differences collectively. For the MANOVA, the null hypothesis tested was the equality of vectors of means of multiple dependent variables (food items) across sucker species. The data were analyzed using SAS (SAS Institute 1990) and Statistica (Statsoft Inc. 1997) software packages. The MANOVA model for comparing sucker species population mean vectors of food items is as follows:

$$(2.13) \quad Y_{ir} = \mu + T_i + \epsilon_{ir}$$
$$i = 1, 2, \ldots, g$$
$$r = 1, 2, \ldots, n_i$$

where Y_{ir} = percent of food category r eaten by sucker species i, μ = overall mean (level), T_i = the ith treatment effects (sucker species) with $n_i T_i = 0$, ϵ_{ir} are independent, normally distributed variables, n_i = prey types eaten by sucker species i, and g = number of sucker species.

The hypotheses used for MANOVA testing are as follows:

$H_o=$ $T_1 = T_2 = \ldots T_g = 0$ (there is no difference in food resource use among sucker species).

$H_A=$ at least one $T_i \neq 0$

Wilk's lambda statistic was used to test the null hypothesis that food use did not differ among sucker species (i.e., the mean population vectors are the same). Wilk's lambda, Λ, was expressed as:

$$(2.14) \quad \Lambda = |W| / |B + W|$$

where $|W|$ = determinant of the residual (error) matrix sum of squares and sum of squares cross products ($SSP = \sum_i \sum_j (x_{ij} - \bar{x}_i)(x_{ij} - \bar{x}_i)'$ with $\sum n_i - g$ degrees of freedom), $|B|$ = determinant of the treatment sum of squares and sum of squares cross

products and is calculated using the equation $\sum_i n_i (\bar{x}_i - \bar{x})(\bar{x}_i - \bar{x})'$ with g-1 degrees of freedom. Equation *2.14* corresponds to an F-test of the following form:

F = (treatment sum of squares/(g-1)) / (residual sum of squares/($\sum n_i$-g))

if the F-value was > $F_{g-1,\sum ni-g}(\propto)$, I rejected the null hypothesis that food use did not differ among sucker species.

Canonical analysis of variates followed a significant MANOVA (Johnson and Wichern 1992). This analysis was used to examine collective differences in food use among sucker species. Canonical is used to assess the composite relationship between multiple dependent and multiple independent variables. Through this procedure, weighted, linear composites of dependent variables (prey categories), called canonical variables, were derived that maximized the difference between the independent (sucker species) variables. Those dependent variables with the highest correlations with the first canonical variable contributed most to the separation of species, as the first canonical variable defined the greatest separation of species (Johnson and Wichern 1992). The two canonical variables that accounted for most of the separation among sucker species were used to form axes. The position of each sucker species on the two canonical variables was portrayed by plotting species scores of food categories on the canonical variables and an ellipse was formed around each set of scores for a species.

The analysis (MANOVA + canonical analysis of variates) assumed equal catchability over species and gear types. Klecka (1975) concluded that this multivariate technique was robust enough that the assumptions of a multivariate normal distribution of discriminating variables and equal variance-covariance matrices between groups need not be rigorously met.

RESULTS

Sucker Community Composition

The YSS and the GOS exhibited greatly different sucker communities, with different dominant species. Suckers were a major component of the total fish catch

in the GOS, but not of the total fish catch in the YSS. In the YSS, 499 suckers were captured, representing seven species (bigmouth buffalo, *Ictiobus cyprinellus*; smallmouth buffalo, *Ictiobus bubalus*; river carpsucker, *Carpiodes carpio*; shorthead redhorse, *Moxostoma macrolepidotum*; white sucker, *Catostomus commersonii*; longnose sucker, *Catostomus catostomus*; and blue sucker, *Cycleptus elongatus*). Suckers were not a major component of the total fish catch. Bigmouth buffalo and smallmouth buffalo constituted 8% and 3% of the total fish catch (sucker and non-sucker species), respectively. River carpsucker made up approximately 2% of the total fish catch, with the other 4 species each contributing less than 1% of total fish catch. Three native species, bigmouth buffalo, smallmouth buffalo, and river carpsucker, represented 94% of the sucker catch in the YSS.

In the GOS 6,217 suckers were captured, representing seven species (bigmouth buffalo, smallmouth buffalo, river carpsucker, shorthead redhorse, white sucker, longnose sucker, blue sucker). Suckers were a major component of the total fish catch in the GOS. Longnose sucker and white sucker, which were rarely sampled in the YSS, represented 76% of the total catch of all fish species and constituted over 98% of the sucker catch in the GOS. The remaining five sucker species made up less than 2% of the total catch in this segment.

Prey Populations

The average zooplankton density for the YSS habitats (251.8 organisms/liter) was approximately 8 times greater than the density of zooplankton in the GOS habitats (32.6 organisms/liter) (ANOVA, $F=6.80$, $P=0.01$). Benthic invertebrate densities were also higher in the YSS (277.0 organisms/m^2) than in the GOS (149.6 organisms/m^2) habitats (ANOVA, $F=6.04$, $P=0.02$).

Zooplankton richness was similar in both study segments (YSS=4.02 prey types per macrohabitat sample unit, GOS=4.14 prey types per macrohabitat sample unit) (ANOVA, $F=3.09$, $P=0.35$), but the YSS habitats had a higher zooplankton diversity (1/D=2.21, equation 2.2) than the GOS (1/D=1.92) (ANOVA, $F=4.27$, $P=0.02$). Benthic invertebrate diversities were similar in the YSS (1/D=1.08) and the GOS (1/D=1.16) (ANOVA, $F=0.98$, $P=0.28$), but the GOS (2.15 prey types per

macrohabitat sample unit) had higher richness than the YSS (1.60 prey types per macrohabitat sample unit) (ANOVA, F=6.45, P=0.0057).

Feeding Ecology and Food Habits

Food Habits

In the YSS, four species of suckers—bigmouth buffalo, river carpsucker, shorthead redhorse, and smallmouth buffalo—were captured frequently enough for quantitative analysis of summer food habits. Bigmouth buffalo, river carpsucker, and smallmouth buffalo ate mostly zooplankton. Crustacea, primarily Cyclopoida and Bosminidae, composed over 75% of the number (equation 2.4) and over 55% of the volume (equation 2.3) of diets for each of the three species (Tables 2.1 and 2.2). Chironomid larvae also contributed significantly to diets of smallmouth buffalo, constituting approximately 18% of the number and 39% of the volume. Shorthead redhorse fed mostly on aquatic insect larvae. Chironomid and Trichoptera larvae accounted for approximately 65% of the number and 80% of the volume of diets of shorthead redhorse. The frequency of occurrence of zooplankton crustacea in stomachs was over 95% (equation 2.5) for bigmouth buffalo, river carpsucker, and smallmouth buffalo (Table 2.3). Cladocera and Copepoda zooplankton were found in approximately 45% of shorthead redhorse stomachs. Chironomid larvae were found in 30% of bigmouth buffalo and river carpsucker stomachs and in 56% and 92% of smallmouth buffalo and shorthead redhorse stomachs, respectively (Table 2.3).

In the YSS, a positive relation was found between the density of Chironomid larvae in the environment and the abundance of larvae in the stomachs of smallmouth buffalo (r=0.64, n=92 fish, P<0.0001), bigmouth buffalo (r=0.64, n=68, P<0.0001), and river carpsucker (r=0.83, n=74 fish, P<0.0001). This relation did not exist between zooplankton density (number/liter) and the abundance of zooplankton found in stomachs of river carpsucker (r=0.08, n=74 fish, P=0.61), smallmouth buffalo (r=0.07, n=92 fish, P=0.55), and bigmouth buffalo (r=0.10, n=68 fish, P=0.57).

In the GOS, four species of suckers—longnose sucker, river carpsucker, shorthead redhorse, and white sucker—were captured frequently enough for quantitative analysis of summer food habits. Shorthead redhorse and white sucker ate mostly Chironomid larvae. Chironomids composed over 60% (equation 2.3) (44% of the number, equation 2.4) and 85% (81% of the number) of the volume of white sucker and shorthead redhorse diets, respectively (Table 2.5). Longnose suckers fed mostly on a combination of filamentous green algae and Chironomid larvae which accounted for over 90% of the volume of food items in the diet. River carpsuckers ate mostly zooplankton. Crustacea, primarily Cyclopoida, constituted over 90% of the number and over 55% of the volume of river carpsucker diets (Tables 2.4 and 2.5). The frequency of occurrence (equation 2.5) for crustacean zooplankton was high in river carpsuckers (97%) and white suckers (51%). Chironomid larvae were found in over 90% of longnose sucker, shorthead redhorse, and white sucker stomachs. Chironomids were found in 64% of river carpsucker stomachs (Table 2.6). Food habits information for blue sucker is also included in Tables 2.4-2.6.

In the GOS, a positive relation was found between the density of Chironomid larvae in the environment and the abundance of larvae in stomachs of river carpsucker (r=0.71, n=84 fish, P<0.0001), white sucker (r=0.53, n=71 fish, P=0.04), and longnose sucker (r=0.60, n=74 fish, P<0.0001). However, this relation did not exist for zooplankton density (number/liter) and the abundance of zooplankton found in stomachs of river carpsucker (r=0.11, n=84 fish, P=0.56) or white sucker (r<0.01, n=71 fish, P=0.98). A positive relation was found, however, for longnose suckers (r=0.80, n=74 fish, P<0.0001).

Electivity

In the YSS, most sucker species positively selected (equation 2.7) for pelagic prey items, mainly Copepoda and Cladocera zooplankton, and negatively selected for most benthic prey items (Table 2.7). The shorthead redhorse was the only sucker to select for large benthic macroinvertebrates (Chironomidae and Trichoptera) in the YSS. In contrast, sucker species in the GOS selected against

most pelagic prey items, but selected for most large benthic macroinvertebrates (Table 2.8).

Feeding Strategy

In the YSS, resource use patterns differed among the four dominant sucker species. River carpsucker and bigmouth buffalo had generalized feeding strategies, as indicated by the high frequency of occurrence and the low prey-specific abundance of many food items in their stomachs (i.e. most points located in the lower right portion of the Costello graph, Figure 2.4) and their relatively wide food niche breadths (equation 2.10) bigmouth buffalo, B_A=0.106; river carpsucker, B_A=0.138). The most important prey taxa (Cyclopoida) had been eaten by more that half the fish of each species, but their average contribution to the diet of these fish was low. Smallmouth buffalo exhibited a more mixed feeding strategy, with varying degrees of specialization and generalization of different prey types (Figure 2.4) and a relatively wide food niche breadth (B_A=0.101).

Shorthead redhorse exhibited a more specialized feeding strategy, towards a single, dominant prey taxon with small proportions of other prey types included occasionally in the diet of some individuals (Figure 2.4). This resulted in a narrow food niche breadth for the species (B_A=0.009).

In the GOS, river carpsucker exhibited a generalized feeding strategy. Nearly all prey taxa, including the important prey types, were less than 50% prey-specific abundance, indicating that many prey items were eaten occasionally and that no single prey taxon was fed on heavily (Figure 2.5). A generalized feeding strategy for this species was further supported by a relatively wide food niche breadth (B_A=0.106).

White sucker, longnose sucker, and shorthead redhorse exhibited a specialized feeding strategy (Figure 2.5). Shorthead redhorse and white suckers fed mostly on Chironomid larvae and longnose suckers fed almost exclusively on two prey taxa, including Chironomid larvae and filamentous green algae. A specialized feeding strategy for these species was further supported by their narrow

food niche breadths (longnose sucker, $B_A=0.046$; shorthead redhorse, $B_A=0.013$; white sucker, $B_A=0.057$).

A positive relation was found between zooplankton diversity in sucker habitats and sucker food niche breadth in both the YSS ($r=0.49$, $P<0.0001$) and the GOS ($r=0.39$, $P=0.0009$). No such relation was found, however, between benthic invertebrate diversity and food niche breadth.

Food Niche Overlap

Food niche overlap between species varied in both the YSS and the GOS (Tables 2.9 and 2.10). In the YSS, overlap was high (R_o greater than 0.66) between bigmouth buffalo and river carpsucker ($R_o=0.94$, equation 2.11), bigmouth buffalo and smallmouth buffalo ($R_o=0.87$), river carpsucker and smallmouth buffalo ($R_o=0.86$), and smallmouth buffalo and shorthead redhorse ($R_o=0.74$) (Table 2.9). Intermediate levels of food niche overlap were found between shorthead redhorse and bigmouth buffalo ($R_o=0.56$) and river carpsucker and shorthead redhorse ($R_o=0.55$).

In the GOS, similar and high degrees of food niche overlap were found between most sucker species. The highest overlap was found between white sucker and shorthead redhorse ($R_o=0.91$), the lowest between longnose sucker and river carpsucker ($R_o=0.49$). Overlap between the remaining species pairs ranged from 0.70 for longnose sucker and shorthead redhorse to 0.80 for shorthead redhorse and white sucker (Table 2.10).

Food use differences existed among sucker species (YSS, MANOVA, Wilk's Lambda=0.4118, $P<0.0001$; GOS, MANOVA, Wilk's Lambda=0.2422, $P<0.0001$), but not years (YSS, MANOVA, Wilk's Lambda=0.8252, $P=0.08$; GOS, MANOVA, Wilk's Lambda=0.9364, $P=0.23$) in each river segment. No significant interaction was found between sucker species and years in the YSS (MANOVA, Wilk's Lambda=0.8391, $P=0.06$) or the GOS (MANOVA, Wilk's Lambda=0.8504, $P=0.37$).

The canonical analysis of food habits in the YSS derived three canonical variables, each a composite of the seven food categories retained (Table 2.11). The first two variables accounted for approximately 97% of the diet differences

among the four species. Trichoptera and Chironomid larvae exhibited the largest scores (standardized canonical coefficients) on the first canonical variable (Trichoptera=0.9515, Chironomid larvae=0.7845) which indicates that both prey types were responsible for most of the diet differences among the four species.

Plots of individual scores on the first two canonical variables resulted in the species separating into two groups (Figure 2.6). One group consisted of the three mainly zooplanktivorous fishes and showed the following order of decreasing dependence on large benthic prey and increasing dependence on small pelagic prey: smallmouth buffalo, river carpsucker, bigmouth buffalo. The second group included the benthic invertivorous shorthead redhorse which showed a strong dependence on large benthic prey. Bigmouth buffalo and river carpsucker showed nearly complete overlap in diet, whereas smallmouth buffalo overlapped with these two species as well as shorthead redhorse.

The canonical analysis of food habits in the GOS derived three canonical variables, each a composite of the nine food categories retained (Table 2.12). The first two variables accounted for approximately 94% of the diet differences among the four species. Filamentous green algae and Cyclopoida exhibited the largest scores (standardized canonical coefficients) on the first canonical variable (filamentous green algae=-0.6912, Cyclopoida=0.4691) which indicates that both prey types were responsible for most of the diet differences among suckers in the GOS.

Plots of individual scores on the first two canonical variables resulted in the species separating into two groups (Figure 2.7). One group consisted of three invertivores and showed the following order of decreasing dependence on filamentous green algae: white sucker, shorthead redhorse, river carpsucker. The second group consisted of the herbivorous and invertivorous longnose sucker which showed a strong dependence on filamentous green algae.

DISCUSSION

Sucker Community Composition

Major differences in river physiochemical conditions and habitat in the two segments were associated with the highly dissimilar Catostomid species communities in the YSS and the GOS. The construction of Garrison Dam and Lake Sakakawea has greatly altered original river conditions in the GOS. After closure of the dam in 1953, hypolimnetic withdrawals from Lake Sakakawea resulted in lower water temperatures in the GOS (Everett 1999). Additionally, the dam and Lake Sakakawea act as a sediment trap. Sediments flowing into Lake Sakakawea settle out behind the dam under reduced current velocities, limiting downstream movement of the river's suspended load which has led to river channel incision (Berkas 1995) and reduced turbidity (Young et al. 1997) in this segment. Channel incision has deepened the main river channel, eliminating periodic connecting of the main river channel with the floodplain. This process has also led to isolation of off-channel habitats, such as large, natural backwaters and oxbow lakes, from the main channel. Conversely, the YSS is characterized by high turbidity, a more shallow and braided main channel, and periodic connection of the main channel with the floodplain and large backwater habitats.

The sucker community in the YSS was dominated by river carpsucker, bigmouth buffalo, and smallmouth buffalo, most of which were captured in several large backwaters. These species have been shown to forage and rear in floodplain river systems that contain large, lacustrine habitats, such as backwaters (Walburg and Nelson 1966, Kay et al. 1994), that are characterized by periodic inundation from high runoff (Cook 1959, Pflieger 1975, Smith 1979). Such floodplain backwaters typified the pre-impoundment middle and lower- Missouri River which was characterized by a sucker community comprised mainly of these three species and others in the genera *Ictiobus* and *Carpiodes* (Funk and Robinson 1974). In rivers and streams, most species in these genera prefer habitat that exhibit slow current velocities, silt/sand bottoms, and some turbidity, conditions that often exist in

pools, backwaters, and oxbow lakes (Pflieger 1975, Cross and Collins 1995). The natural Missouri River habitats and physiochemical conditions that these species prefer still exist in the YSS and are responsible for their high abundance.

Conversely, the GOS was dominated by white suckers and longnose suckers that are most often found in streams and lakes that are characterized by very clear, cool water (Scott and Crossman 1973). The preferred temperature range for longnose suckers is 10-15 °C (Brown and Graham 1953) with the upper lethal temperature (50% mortality in 24 hours) for this species near 27 °C (Black 1953). White suckers can tolerate warmer water temperatures than longnose suckers. The preferred temperature range for white sucker was 19-21 °C in a Colorado reservoir (Horak and Tanner 1964) and experimental evidence suggests that an optimum summer water temperature for this species is 24 °C (Reynolds and Casterlin 1978). Both species also seem to survive best in very clean and clear water (Edwards 1983, Twomey and Nelson 1984). Water temperatures rarely exceeded 16 °C in the main channel and 18 °C in off-channel habitats in the GOS , but frequently exceeded 23 °C in these habitats in the YSS (Young et al. 1997). The YSS has a high silt load and is very turbid (mean turbidity=147.3 NTU), whereas the GOS possesses very clear, low turbidity water (mean turbidity=8.4 NTU; Young et al. 1997). Warm water temperatures and high turbidity most likely limited longnose sucker and white sucker numbers in the YSS, whereas cool water temperatures and low turbidity facilitated their high abundance in the GOS.

Minor alterations to river systems have often led to changes in growth (Orlova 1988, Beamesderfer et al. 1995), habitat use (Heggenes 1988, Pert and Erman 1994), or patterns of recruitment (Crisp et al. 1983, Schlosser 1985, Rulifson and Manooch III 1990, Baran et al. 1995) for native species of fish. However, species replacement has occurred in rivers which have sustained more intense anthropogenic disturbances (Winston and Taylor 1991, Martinez et al. 1994, Schmidt et al. 1998). The drastic changes in habitat and physiochemical conditions in the GOS have evidently led to replacement of native sucker species that thrive in

river conditions that typified the pre-control Missouri River with species that thrive in systems characterized by cool, clear water.

Feeding Ecology and Food Habits

An objective of this study was to determine if anthropogenic disturbances influence aspects of sucker feeding ecology by studying and comparing two sucker communities--one influenced by relatively natural river conditions and the other influenced by extensive man-made alterations. This question could be best answered if the comparison was made between communities that exhibited identical, or nearly identical, sucker species compositions. The habitat in the GOS had been so extensively altered, however, that the two sucker communities were highly dissimilar, thereby preventing the comparison of sucker communities that contained the same species. Therefore it was only possible to pursue the comparison using two highly dissimilar sucker communities.

Collectively, the dominant sucker species in the YSS (bigmouth buffalo, river carpsucker, and smallmouth buffalo) tended to exhibit greater food use overlap (Tables 2.7 and 2.8), a higher degree of zooplanktivory (Tables 2.1 and 2.4), and wider food niche breadths than the dominant species in the GOS (longnose sucker, river carpsucker, white sucker). Zooplankton density was high (251.8 organisms/liter) in the YSS habitats. The diets of trophic competitors, such as suckers, are expected to converge when prey is abundant and to diverge in times of low food availability, a pattern documented by Zaret and Rand (1971), Werner and Hall (1976), and Horn (1983). Further, other researchers have maintained that for certain fish communities a dense invertebrate prey resource base results in opportunistic feeding and a lack of food resource partitioning (Martin 1984, Schlosser and Toth 1984). Of the dominant species in the YSS, the bigmouth buffalo is the only species considered to be a strict zooplanktivore (Pflieger 1975, Cross and Collins 1995), although even this species has been known to feed opportunistically on non-zooplankton prey when these prey items were in high abundance (Tafanelli et al. 1971). River carpsucker and smallmouth buffalo are generally considered to be benthic invertivores (Pflieger 1975, Cross and Collins

1995). However, like the bigmouth buffalo, these species have been known to feed opportunistically on alternative prey, such as zooplankton, when in high abundance (Walburg and Nelson 1966, McComish 1967, Vainio 1973). Evidently, the high density of zooplankton in the YSS resulted in bigmouth buffalo, smallmouth buffalo, and river carpsucker feeding more heavily on zooplankton than on other prey items, which led to high food use overlap.

The lack of zooplanktivory by the GOS sucker species may have resulted from morphological constraints. Longnose sucker, river carpsucker, and white sucker possess adaptations for a benthic existence, such as a sub-terminal mouth, that may effectively limit the availability of a food resource that is distributed in the water column. However, longnose sucker and white sucker have been shown to be strict zooplanktivores when this resource was abundant (Barton 1980) and zooplankton dominated the diet of river carpsucker in the YSS, another species that usually exhibits benthivorous feeding habits (Buchholz 1957, Brezner 1958). Therefore, the availability of zooplankton, not fish morphology, likely limited the use of this food resource by suckers in the GOS. Furthermore, the low density of both zooplankton and other invertebrate prey caused species there to feed on a greater variety of prey resulting in greater food resource partitioning than in the YSS.

Food niche breadths in both the YSS and the GOS increased as the diversity of zooplankton increased (YSS, $r=0.49$, $P<0.0001$; GOS, $r=0.39$, $P=0.0009$), but this same relationship did not exist between food niche breadths and benthic invertebrate prey diversity in these two river segments. Food niche breadth quantifies the diversity or breadth of the food resource gradient utilized by a given species (Siaw-Yang 1988). Therefore, if fish feed on a diverse group of organisms, their niche breadths should be wider than fish species that feed on a less diverse prey community. The dominant sucker species in the YSS fed on a readily available and diverse zooplankton food source. This food resource was also diverse in the GOS, but was of limited importance to suckers in the GOS because of its low availability. The major dietary component of sucker diets in the GOS was benthic invertebrates which exhibited low diversity. Therefore, the high availability of a

diverse zooplankton prey source in the YSS and the low availability of zooplankton and the low diversity of invertebrate prey in the GOS are apparently responsible for segment differences in food niche breadths.

Results from this study indicate that the feeding ecology differed between the two sucker communities and that higher invertebrate prey densities were directly responsible for the greater food niche overlap and indirectly responsible for the greater food niche breadths found for suckers in the YSS. However, the mechanisms responsible for the difference in prey densities between segments are less clear. In the Missouri River, dam construction and other alterations, such as bank stabilization, have reduced sediment transport and deposition and virtually eliminated the processes of flooding and meandering of the main channel (Hesse et al. 1989, Hesse and Sheets 1993). Elimination of these conditions has reduced the formation of backwater and wetland habitat and drastically reduced available supplies of carbon in the GOS and other Missouri River segments (Hesse et al. 1988). Changes in carbon supplies and in the availability of off-channel habitats have reduced invertebrate productivity in segments of the Missouri River altered by dams (Hesse et al. 1988). Further, disruption of these processes has changed channel substrates, making them less conducive to benthic production (Berner 1951). Changes in these natural Missouri River processes probably explains why invertebrate prey densities, particularly zooplankton densities, were much lower in the GOS habitats. Invertebrate communities undoubtedly benefit from the natural Missouri River conditions and processes that still exist in the YSS, but are now absent or reduced in the GOS.

The low occurrence of native Missouri River suckers and the low density of potential sucker prey in the GOS indicates that this segment is not good habitat for most native suckers. Therefore, restoring natural river conditions, such as a high sediment load, channel meandering, and a periodic flood pulse, that maintain natural prey populations and a diversity of natural habitats is critical for the survival of native sucker species in the GOS and other altered Missouri River segments.

LITERATURE CITED

Amundsen, P. A., H. M. Gabler, and F. J. Staldvik. 1996. A new approach to graphical analysis of feeding strategy from stomach contents data — modification of the Costello (1990) method. Journal of Fish Biology 48: 607-614.

Anderson, K. A., T. L. Beitinger, and E. G. Zimmerman. 1983. Forage fish assemblages in the Brazon River upstream and downstream from Possum Kingdom Reservoir, Texas. Journal of Freshwater Ecology 2: 81-88.

Baran, P., M. Delacoste, F. Dauba, J.-Marc Lascaux, A. Belaud, and S. Lek. 1995. Effects of reduced flow on brown trout (*Salmo trutta* L.) populations downstream dams in French Pyrenees. Regulated Rivers: Research and Management 10: 347-361.

Barton, B. A. 1980. Spawning migrations, age and growth, and summer feeding of white and longnose suckers in an irrigation reservoir. The Canadian Field-Naturalist 94: 300-304.

Beamesderfer, R. C. P., T. A. Rien, and A. A. Nigro. 1995. Differences in the dynamics and potential production of impounded and unimpounded white sturgeon populations in the lower Columbia River. Transactions of the American Fisheries Society 124: 857-872.

Berner, L. M. 1951. Limnology of the lower Missouri River. Ecology 32: 1-12.

Berkas, W. R. 1995. Transport and sources of sediment in the Missouri River between Garrison Dam and the headwaters of Lake Oahe, North Dakota, May 1988 through April 1991. Water-resources investigations report 95-4087. U. S. Department of the Interior, U. S. Geological Survey, Bismarck, North Dakota.

Black, E. C. 1953. Upper lethal temperatures of some British Columbia freshwater fishes. Journal of the Fisheries Research Board of Canada 10: 196-210.

Box, G. E. P. 1949. A general distribution theory for a class of likelihood criteria. Biometrika 36: 317-346.

Brezner, J. 1958. Food habits of the northern river carpsucker in Missouri. The Progressive Fish-Culturist 20: 170-174.

Brown, C. J. D., and R. J. Graham. 1953. Observations on the longnose sucker in Yellowstone Lake. Transactions of the American Fisheries Society 83: 38-46.

Buchholz, M. 1957. Age and growth of river carpsucker in Des Moines River, Iowa. Iowa Academy of Science 64: 589-600.

Cambray, J. A., J. M. King, and C. Bruwer. 1997. Spawning behaviour and early development of the clanwilliam yellowfish (Barbus capensis; Cyprinidae), linked to experimental dam releases in the Olifants River, South Africa. Regulated Rivers: Research and Management 13: 579-602.

Cook, F. A. 1959. Freshwater fishes in Mississippi. Mississippi Game and Fish Commission, Jackson.

Crisp, D. T., R. H. K. Mann, and P. R. Cubby. 1983. Effects of regulation of the River Tees upon fish populations below Cow Green Reservoir. Journal of Applied Ecology 20: 371-386.

Cross, F. B, and J. T. Collins. 1995. Fishes in Kansas. Museum of Natural History, Public Education Series, No. 14, University of Kansas, Lawrence.

Dumont, H. J., I. Van de Veld, and S. Dumont. 1975. The dry weight estimate of biomass in a selection of Cladocera, Copepoda, and Rotifera from the plankton, periphyton, and benthos of continental waters. Oecologia 19: 75-97.

Edwards, E. A. 1983. Habitat suitability index models: longnose sucker. U. S. Fish and Wildlife Service Report No. FWS/OBS-82/10.35. Fort Collins, Colorado.

Everett, S. R. 1999. Ecology and life history of three native benthic fishes in the Missouri and Yellowstone River. Master's thesis. University of Idaho, Moscow.

Funk, J. L., and J. W. Robinson. 1974. Changes in the channel of the lower Missouri River and effects on fish and wildlife. Missouri Department of Conservation, Aquatic Series No. 11, Jefferson City.

Galat, D. L., L. H. Fredrickson, D. D. Humburg, K. J. Bataille, J. R. Bodie, J. Dohrenwend, G. T. Gelwicks, J. E. Havel, D. L. Helmers, J. B. Hooker, J. R. Jones, M. F. Knowlton, J. Kubisiak, J. Mazourek, A. C. McColpin, R. B.

Renken, and R. D. Semlitsch. 1998. Flooding to restore connectivity of regulated, large-river wetlands. Bioscience 48: 721-747.

Gray, E. V., J. M. Boltz, K. A. Kellogg, and J. R. Stauffer, Jr. 1997. Food resource partitioning by nine sympatric darter species. Transactions of the American Fisheries Society 126: 822-840.

Heggenes, J. 1988. Effects of short-term flow fluctuations on displacement of, and habitat use by, brown trout in a small stream. Transactions of the American Fisheries Society 117: 336-344.

Helfman, G. S., B. B. Collette, and D. E. Facey. 1997. The diversity of fishes. Blackwell Science, Malden, Massachusetts.

Hesse, L. W., and C. W. Wolfe, and N. K. Cole. 1988. Some aspects of energy flow in the Missouri River ecosystem and a rationale for recovery. Pages 13-29 *in* N. G. Benson, editor. The Missouri River-- the Resources, Their Uses, and Values. North Central Division American Fisheries Society, Special Publication 8, Bethesda, Maryland.

Hesse, L. W., J. C. Schmulbach, J. M. Carr, K. D. Keenlyne, D. G. Unkenholz, J. W. Robinson, and G. E. Mestl. 1989. Missouri River fishery resources in relation to past, present, and future stresses. Pages 352-371 *in* D. P. Dodge, editor. Proceedings of the International Large River Symposium. Canadian Special Publications of Fisheries and Aquatic Science, 106, Ottawa, Ontario, Canada.

Hesse, L. W., and W. Sheets. 1993. The Missouri River hydrosystem. Fisheries 18(5): 5-14.

Hill, M. O. 1973. Diversity and evenness: a unifying notation and its consequences. Ecology 54: 427-432.

Horak, D. L., and H. A. Tanner. 1964. The use of vertical gill nets in studying fish depth distribution, Horsetooth Reservoir, Colorado. Transactions of the American Fisheries Society 93: 137-145.

Horn, H. S. 1966. Measurement of "overlap" in comparative ecological studies. American Naturalist 100:419-424.

Horn, H. H. 1983. Optimal diets in complex environments: feeding strategies of two herbivorous fishes from a temperate rocky intertidal zone. Oecologia 58: 345-350.

Hyslop, E. J. 1980. Stomach contents analysis - a review of methods and their application. Journal of Fish Biology 17: 411-429.

Johnson, R. A., and D. W. Wichern. 1992. Applied multivariate statistical analysis. Prentice Hall, New Jersey.

Kay, L. K., R. Wallus, and B. L. Yeager. 1994. Reproductive biology and early life history of fishes in the Ohio River drainage, Volume 2. Tennessee Valley Authority, Chattanooga.

Klecka, W. H. 1975. Discriminant analysis. Page 435 *in* N. H. Nie, C. H. Hall, T. G. Jenkins, K. Steinbrenner, and D. H. Brent, editors. Statistical Package for the Social Sciences, 2nd edition. McGraw-Hill, New York.

Levins, R. 1968. Evolution in changing environments. Princeton University Press, Princeton, New Jersey.

Litvak, M. K., and R. I. C. Hansell. 1990. Investigation of food habit and niche relationships in a cyprinid community. Canadian Journal of Zoology 68: 1873-1879.

Martin, F. D. 1984. Diets of four sympatric species of *Etheostoma* (Pisces: Percidae) from southern Indiana: interspecific and intraspecific multiple comparisons. Environmental Biology of Fishes 11: 113-120.

Martinez, P. J., T. E. Chart, M. A. Trammell, J. G. Wullschleger, and E. P. Bergersen. 1994. Fish species composition before and after construction of a main stem reservoir on the White River, Colorado. Environmental Biology of Fishes 40: 227-239.

McComish, T. S. 1967. Food habits of bigmouth and smallmouth buffalo in Lewis and Clark Lake and the Missouri River. Transactions of the American Fisheries Society 96:70-74.

Miller, R. R. 1959. Origin and affinities of the freshwater fish fauna of western North America. Pages 187-222 *in* C. L. Hubbs, editor. Zoogeography. Washington, D. C.: National Academy of Science.

Minckley, W. L., J. E. Johnson, J. N. Rinne, and S. E. Willoughby. 1970. Foods of buffalofishes, Genus *Ictiobus*, in Central Arizona reservoirs. Transactions of the American Fisheries Society 99: 333-342.

Minckley, W. L. 1991. Native fishes of the Grand Canyon region: An obituary? Pages 124-177 *in* G. R. Marzolf, editor. Colorado River Ecology and Dam Management. Washington, D. C.: American Association for the Advancement of Science.

Orlova, E. L. 1988. Peculiarities of growth and maturation of the catfish, *Silurus glanis*, in the Volga Delta under regulated flow conditions. Journal of Ichthyology 28: 35-45.

Pert, E. J., and D. C. Erman. 1994. Habitat use by adult rainbow trout under moderate artificial fluctuations in flow. Transactions of the American Fisheries Society 123: 913-923.

Pflieger, W. L. 1975. The fishes of Missouri. Missouri Department of Conservation, Jefferson City.

Reynolds, W. W., and M. E. Casterlin. 1978. Behavioral thermoregulation and diel activity in white sucker (*Catostomus commersoni*). Comparative Biochemistry and Physiology A. Comparative Physiology 59: 261-262.

Rulifson, R. A., and C. S. Manooch III. 1990. Recruitment of juvenile striped bass in the Roanoke River, North Carolina, as related to reservoir discharge. North American Journal of Fisheries Management 10: 397-407.

SAS. 1990. SAS System. SAS Institute Inc., Cary, North Carolina.

Schlosser, I. J. 1985. Flow regime, juvenile abundance, and the assemblage structure of stream fishes. Ecology 66: 1484-1490.

Schlosser, I. J., and L. A. Toth. 1984. Niche relationships and population ecology of rainbow (*Etheostoma caeruleum*) and fantail (*E. flabellare*) darters in a temporally variable environment. Oikos 42: 229-238.

Schmidt, J. C., R. H. Webb, R. A. Valdez, G. R. Marzolf, and L. E. Stevens. 1998. Science and values in river restoration in the Grand Canyon. Bioscience 48: 735-747.

Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada, Bulletin 184, Ottawa, Ontario, Canada.,

Smith, P. W. 1979. The fishes of Illinois. University of Illinois Press, Urbana.

Smock, L. A. 1980. Relationships between body size and biomass of aquatic insects. Freshwater Biology 10: 375-383.

Siaw-Yang, Y. 1988. Food resource utilization partitioning of fifteen fish species at Bukit Merah Reservoir, Malaysia. Hydrobiologia 157: 143-160.

Statsoft, Inc. 1997. Statistica user's guide. 1997 edition. Statsoft Inc. Tulsa, Oklahoma.

Strauss, R. E. 1979. Reliability estimates for Ivlev's Electivity Index, the forage ratio, and a proposed linear index of food selection. Transactions of the American Fisheries Society 108:344-352.

Tafanelli, R., P. E. Mauck, and G. Mensinger. 1971. Food habits of bigmouth and smallmouth buffalo from four Oklahoma Reservoirs. Proceedings of the Twenty-fourth Annual Conference Southeastern Association of Game and Fish Commissioners: 649-658.

Trautman, M. B. 1957. The fishes of Ohio. The Ohio State University Press, Columbus.

Twomey, K. A., and K. L. Williamson. 1984. Habitat suitability index models and instream flow suitability curves: white sucker. U. S. Fish and Wildlife Service Report No. FWS/OBS-82/10.35. Fort Collins, Colorado.

Vainio, P. W. 1973. Feeding and food habits of the smallmouth buffalo, *Ictiobus bubalus* (Rafinesque), in Elephant Butte Lake, New Mexico. Master's thesis, New Mexico State University, Las Cruces.

Walburg, C. H., and W. R. Nelson. 1966. Carp, river carpsucker, smallmouth buffalo, and bigmouth buffalo in Lewis and Clark Lake, Missouri River. U. S. Department of the Interior, Fish and Wildlife Service, Bureau of Sport Fisheries and Wildlife Research Report 69.

Werner, E. E., and D. J. Hall. 1976. Niche shifts in sunfishes: experimental evidence and significance. Science 191: 404-406.

Winston, M. R., and C. M. Taylor. 1991. Upstream extirpation of four minnow species due to damming of a prairie stream. Transactions of the American Fisheries Society 120: 98-105.

Young, B. A., T. L. Welker, M. L. Wildhaber, C. R. Berry, and D. Scarnecchia, editors. 1997. Population structure and habitat use of benthic fishes along

the Missouri and Lower Yellowstone River. 1997 Annual Report of Missouri River Benthic Fish Study PD-95-5832 to the U. S. Army Corps of Engineers and the U. S. Bureau of Reclamation.

Zaret, T. M., and A. S. Rand. 1971. Competition in tropical stream fishes: support for the competitive exclusion principle. Ecology 52: 336-342.

CHAPTER 3

Habitat Use and Population and Community Structure of
Native Fishes in the Upper Missouri and
Lower Yellowstone Rivers, North Dakota

ABSTRACT

In 1997 and 1998, sampling was conducted on the Missouri and Yellowstone Rivers, North Dakota to examine the influence of anthropogenic disturbance on the fish community and to obtain information on the distribution, abundance, and habitat use of the flathead chub (*Platygobio gracilis*), sicklefin chub, (*Macrhybopsis meeki*), sturgeon chub (*Macrhybopsis gelida*), and western silvery minnow (*Hybognathus argyritis*), four declining fish species (Family Cyprinidae) native to the Missouri River basin. The study area consisted of four distinct river segments, the Missouri River between its confluence with the Yellowstone River and the Montana-North Dakota border (the above confluence segment; ACS), a flow regulated, moderately altered segment, the Missouri River between its confluence with the Yellowstone River and Lake Sakakawea (the below confluence segment; BCS), a moderately altered segment, the Yellowstone River near its confluence with the Missouri River (the Yellowstone River segment; YRS), a quasi-natural segment, and the Missouri River at the Missouri River-Yellowstone River confluence (the mixing zone segment; MZS). Catch rates with the trawl for sicklefin chub and sturgeon chub and catch rates with the bag seine for flathead chub and western silvery minnow were highest in the BCS and YRS. Most sicklefin chubs and sturgeon chubs were captured in main channel habitat with the trawl (sicklefin chub=97%, sturgeon chub=85%), whereas most flathead chub and western silvery minnow were captured in channel border habitat with the bag seine (flathead chub=99%, western silvery minnow=98%). Best-fit regression models predicted sicklefin chub, flathead chub, and western silvery minnow presence and absence correctly greater than eighty percent of the time. Sturgeon chub presence and absence was predicted correctly fifty-five percent of the time. Best-fit regression models fit to fish number data for

flathead chub, sicklefin chub, and sturgeon chub and fish catch-per-unit-effort data for flathead chub also provided good fits with R^2 values ranging from 0.32 to 0.55. The more natural river conditions (i.e., high turbidity and hydrographs typified by a spring flood peak) in the YRS and BCS made these two segments better habitat for native species of fish than the ACS and MZS.

INTRODUCTION

The physical and biological characteristics of riverine systems have been shown to shape fish communities (Kuehne 1962, Barila, et al. 1981). Alterations of these river characteristics have led to subsequent changes in fish populations (Walker and Thoms 1993, Duque et al. 1998) and fish community structure (Bain 1985, Layher 1994, Schmidt et al. 1998, Penaz et al. 1999). In many large river systems, dams have been primarily responsible for changes in downstream river physical habitat characteristics (e.g., depth, turbidity, and water temperature), resulting in changes in native fish species distribution, abundance, and community structure (Minckley 1991, Ligon et al. 1995, Gehrke et al. 1999).

Historically, most sections of the Missouri and lower Yellowstone Rivers possessed very similar physical characteristics, including high sediment loads, meandering channels, and fluctuating hydrographs. Today, the hydrological, physical, and biological characteristics of many Missouri River segments have been altered from dam construction, bank stabilization, and other actions; impacted river segments often exhibit very different environmental characteristics and fish communities from those of unaltered segments (Hesse et al. 1989).

The confluence of the Missouri and Yellowstone Rivers occurs in northwest North Dakota near the Montana-North Dakota border. Many native species of fish are abundant in the confluence area, but are considered at risk or threatened in other portions of the Missouri River basin (Hesse et al. 1989). The lower Yellowstone River below the Intake Diversion Dam (river km 114.4) is still very turbid and productive, with no dams. Conversely, the Missouri River above the confluence has been impacted by Fort Peck Dam; this segment has an altered hydrograph, a reduced sediment load, and a colder temperature regime (Young et al. 1997). The Missouri River below the confluence is influenced by both the lower Yellowstone

River and Fort Peck Dam. Additionally, at the confluence of the Yellowstone and Missouri Rivers there is a mixing zone of the two rivers resulting in a habitat with physical attributes unlike the other three confluence river segments. These four segments of river thus exhibit different physical, and perhaps biological, characteristics. The distinctiveness and close proximity of these segments provide an opportunity to examine the relationship between an array of environmental variables and the distribution, abundance, and habitat use of various fish species constituting the native fish community.

Several small cyprinid species common to the confluence area have diminished in distribution and abundance in many other segments of the Missouri River and its tributaries (Pflieger and Grace 1987, Hesse 1994). These species include the flathead chub (*Platygobio gracilis*), sicklefin chub (*Macrhybopsis meeki*), sturgeon chub (*Macrhybopsis gelida*), and western silvery minnow (*Hybognathus argyritis*). Concerns over reduction in range of the sicklefin and sturgeon chubs prompted petitions to the United States Fish and Wildlife Service in 1994 to list these two species as endangered. Although the flathead chub and western silvery minnow are not currently being considered for listing under the Endangered Species Act, they are listed by most states as threatened or species of concern (Hesse et al. 1989). Even though numerous researchers (Ozanne 1972, Pflieger 1975, Reigh and Elsen 1979, Stewart 1981, Werdon 1992, Gould 1994, Hesse 1994, Grisak 1996) have provided information on the microhabitat preferences of these native cyprinid fishes, detailed quantitative assessments are absent concerning their habitat use in relation to environmental features of large rivers. In the Missouri River, key questions that remain to be answered are how habitat differences may be manifested in differences in fish community structure and how threatened, native cyprinids are partitioning available habitat. Answers to these questions are best obtained over a very short geographic range where problems with confounding factors are fewer.

The objectives of this study were to: 1) examine fish species abundance, fish species distribution, and fish community structure in four distinct large river segments in the Yellowstone-Missouri River confluence area; 2) examine habitat use and habitat distinctiveness of four native cyprinids during summer; 3) assess the importance of the mixing zone of the Missouri and Yellowstone Rivers to native species of fish.

STUDY AREA

The confluence of the Missouri and Yellowstone Rivers is located in northwest North Dakota, approximately eight kilometers (km) from the North Dakota-Montana border (Figure 3.1). Within the confluence area, two sections of the Missouri River, one section of the Yellowstone River, and the mixing zone of the Missouri and Yellowstone Rivers were the study segments (Figure 3.2). The first segment of the Missouri River extends 8.0 km upriver from the Missouri River and Yellowstone River confluence (Missouri River km 2546; hereafter referred to as the confluence) and is hereafter referred to as the above confluence segment (ACS; Figure 3.2). The second Missouri River segment extends 48.3 km down river from the confluence to the headwaters of Lake Sakakawea (rkm 2470.3) and is hereafter referred to as the below confluence segment (BCS; Figure 3.2). The Yellowstone River segment extends 24.0 km up river from the confluence and is hereafter referred to as the Yellowstone River segment (YRS; Figure 3.2). The mixing zone, hereafter referred to as the mixing zone segment (MZS), extends from the confluence down river approximately 800 m in the Missouri River.

METHODS

Data Collection

Sample Design

Two habitat types, main channel and main channel border, were common to all four study segments and were sampled to characterize segment fish communities and to examine the relationships among fish and select physiochemical variables. Main channel habitat extended longitudinally to the shoreline at and immediately adjacent to the thalweg. Channel border habitat was shallower, and extended laterally from the river shoreline to a maximum depth of 1.5 m.

Eight-250 m sample units that each contained both habitat types were selected near the confluence in each of three segments of river (ACS, BCS, YRS; Figure 3.2). A sample unit was defined as one-250 m stretch of river with its

longitudinal boundaries as the shoreline (Figure 3.2). Sample units were confined within the mainstem river, located between, but not within, inside-outside bend complexes. Only two sample units of this length existed in the MZS, the shortest segment, so only these two sample units were used. Data were collected in the period July-September,1997 and 1998. Two sample units were randomly selected, without replacement, in each of the summer months from each study region. Both available sample units in the MZS were sampled once in each of the three months. In each month, all sample units were sampled within four consecutive days.

Fish Collection

Two gears were used to sample fish within sample units. Fish in main channel habitat were sampled with a benthic beam trawl (2 m in width x 0.5 m in height x 5.5 m in length; 0.32 cm inner mesh; 3.81 cm outer chafing mesh; 16.5 cm cod-end opening) and fish in channel border habitat were sampled with a bag seine (10.7 m in length x 1.8 m in height; 1.8 m³ bag; 5 mm ace mesh).

Three trawl subsamples were taken in main channel habitat in each selected sample unit. For each subsample, the trawl was attached to the bow of the boat and towed downstream (in reverse) beginning at the upstream lateral boundary and proceeding downstream parallel to the shoreline, ending 150 m downstream from the upstream lateral boundary. The first sample was taken in the thalweg, and a coin toss was used to determine whether the second or third was to the left or right of the first (Figure 3.2). A buoyed 150 m anchored line marked the upstream and downstream lateral boundaries and the distance to be towed for each subsample.

Two bag seine subsamples were taken in each sample unit. The first was taken on either shoreline at the one-third point upstream of the downstream lateral boundary of the sample unit and the second was taken on the same shoreline at the two-third point upstream from the downstream lateral boundary (Figure 3.2). The seine was deployed by holding one end stationary and pulling the other end upstream until it was fully extended along the shoreline. The upstream end was then pulled downstream through the water in a 180-degree arc, keeping the net fully extended or until the water column exceeded a depth of 1.5 m. At the end of the arc, the net was pulled to shore.

The number and type of fish captured were recorded. Catch densities of all species were calculated by segment. One seine haul or one trawl tow defined one

unit of sampling effort. All flathead chubs, sicklefin chubs, sturgeon chubs, and western silvery minnows were measured for total length. Length-frequency histograms were constructed for flathead chub, sicklefin chub, sturgeon chub, and western silvery minnow to examine the population structure and assess year class strength within each study segment.

Habitat Characterization

Five physiochemical variables (depth, velocity, turbidity, temperature, and substrate) and one biological variable (invertebrate drift density) were measured after each benthic trawl and each bag seine subsample. An additional biological variable, benthic invertebrate density, was measured after each bag seine subsample. In main-channel habitat, preliminary observations indicated a uniformity of the physiochemical and biological variables among 150 m benthic trawl subsamples; it was therefore decided that single point measurement of these variables, with the exception of depth and velocity, adequately represented the conditions encountered by fish. Depth and velocity were measured at points one-third, one-half, and two-thirds of the tow length upstream from the downstream tow lateral boundary. The three measurements were then averaged to obtain the mean depth and the mean velocity for the tow.

After completing a trawl, the boat was anchored and current velocity was measured with the aid of an A55M sounding reel (Rickly Hydrological Company) and hangar bar (19.1 mm x 304.8 mm). The Marsh-McBirney Flowmate Model 2000 probe was attached to the hangar bar and lowered near bottom with the sounding reel. A 22.7 kg sounding weight was used to keep the current velocity meter probe pointed into the current and positioned directly below the boat. Current velocity was measured to the nearest 0.1 m/sec.

Water temperature was measured with a YSI 30 temperature/conductivity meter. The meter probe was held 1-2 feet under the water's surface and temperature was measured to the nearest 0.1 °C. Water depth was measured with a Lowrance sonar device to the nearest 0.1 m. For turbidity measurements, a sample of water was collected approximately 0.5 m below the water's surface and stored in a vial. Water turbidity was measured with a Hach 2100P turbidity meter to the nearest 1.0 Nephalometric Turbidity Unit (NTU).

A bottom substrate sample was collected with an iron pipe that had one end closed. One end of a nylon rope was attached to the open end of the pipe and the other connected to the boat. The pipe was then dragged upstream 150 m through the path of the trawl tow. The pipe contents were emptied onto the boat and the percentages of silt (particle size <= 0.06 mm), sand (particle size 0.06 <= 2.0 mm), and gravel (particle size 2.0 mm <= 16 mm) were estimated visually.

In main-channel habitat, invertebrate drift was collected with a Wisconsin-style plankton net (10.8 cm diameter, 80 μm mesh) fitted with a General Oceanics flow meter. The boat was anchored and the plankton net was attached to the hangar bar and 22.7 kg sounding weight and lowered to near bottom with the A55M sounding reel. The net remained suspended at this depth for 2 min. The quantity of water sampled by the net was determined using the flow meter and used to calculate the invertebrate density, expressed as number of organisms/liter.

In channel border habitat, the five physiochemical variables and benthic invertebrate drift were measured with the same devices at each bag seine subsample. Water column depth and water velocity were measured along a transect perpendicular to the shore at the mid-point of the 180-degree bag seine arc. Measurements for each variable were taken 2, 6, and 10 m from the shoreline. If the water was too deep and the seine did not extend 10 m from the bank, then depth and current velocity was measured at the greatest distance from the shore that was seined. Depth and velocity were also measured at the 2 and 6 m points if they were less than the greatest distance seined. Depth and current velocity measurements were averaged to obtain an estimate of depth and velocity for the subsample. Water temperature, turbidity, and conductivity were measured at the center of the area seined. A substrate sample was collected with the iron pipe by first placing it at the deepest point seined and dragging it towards shore along the perpendicular transect at the seine midpoint. Percentages of sand, silt, and gravel were then estimated from the pipe contents.

Benthic drift invertebrates were sampled by attaching the Wisconsin-style plankton net to a wooden pole, held perpendicular to a person's body, and towing the net by hand at the site for a period of three minutes. Invertebrate density was expressed as number of organisms/liter.

Benthic macroinvertebrates were sampled with a Ponar dredge (22.9 cm x 22.9 cm). Three Ponar grabs were made at each gear subsample at the 2, 6, and

10 m points along the transect perpendicular to the midpoint of the seine sample. The three samples were combined and invertebrates were separated from substrate by washing grab contents through a wash bucket fitted with a 541 µm sieve screen bottom. The remaining sediment, debris, and macroinvertebrates were placed into a container and preserved with 95% ethanol for transport to the lab and subsequent analysis. In the lab, benthic invertebrates were identified in most cases to family. Invertebrate density was expressed as number of organisms/m^2.

Analyses

Segment and Habitat Characterization

The degree of physiochemical similarity among the four segments was examined with cluster analysis. Cluster analysis was performed on physiochemical data (depth, current velocity, turbidity, temperature, substrate composition, and discharge) measured in each study segment. In each year and segment, physiochemical variables were first averaged within each habitat type and then converted to standard scores by subtracting the mean and dividing by the standard deviation for each variable (Hair et al. 1995). Next, yearly means for segments were obtained for each standardized variable by averaging across the two habitat types. Finally, yearly means were averaged and a 4 x 8 (4 segments x 8 variables) matrix was formed for analysis.

A joining clustering method was employed, with a single linkage amalgamation rule and a Euclidean type distance measure used to form clusters (Hair et al. 1995). Two of the physiochemical variables, depth and velocity, were highly correlated (r>0.90), so a type of Euclidian distance measure, Mahalanobis distance was used (Mahalanobis 1936). Other distance measures were also used and compared to the Mahalanobis measure.

Distinctiveness of habitats among segments was determined with a multivariate technique. Multivariate analysis of variance (MANOVA; Johnson and Wichern 1992) was conducted across segments for each habitat type. Segments and years served as the independent variables and water physiochemical categories (depth, current velocity, turbidity, temperature, percent silt, percent sand) served as the dependent variable.

(3.1) $Y_{ikr} = \mu + T_i + \beta_k + Y_{ik} + e_{ikr}$

$i = 1, 2, \ldots, g$

$k = 1, 2$

$r = 1, 2, \ldots, n$

where Y_{ikr} = is physiochemical category r for year k in segment i, μ = overall mean (level), T_i = the segment i effect, β_k = the year k effect, Y_{ik} = interaction between segments and years, e_{ikr} are independent, normally distributed variables, g = number of segments, and n = number of physiochemical categories.

The hypotheses used for MANOVA testing are as follows:

$H_o=$ $T_1 = T_2 = \ldots T_g = 0$ (there is no difference in habitat characteristics among segments).

$H_A=$ at least one $T_i \neq 0$

The equal variance-covariance assumption was checked with the Box test (Box 1949) Residual plots for each dependent variable were constructed to examine homoscedasticity. Multicollinearity between dependent variables was examined by computing the variance inflation factor. An appropriate transformation, such as arcsine (square root (y)), log (y+1), or square root (y), was applied to dependent variables that violated any of the assumptions (Hair et al. 1995).

Canonical analysis of variates followed a significant MANOVA (Johnson and Wichern 1992). This analysis was used to examine collective differences in habitats among segments. Canonical analysis of variates is used to assess the composite relationship between multiple dependent and multiple independent variables. Through this procedure, weighted, linear composites of dependent variables (physiochemical categories), called canonical variables, were derived that maximized the difference between the independent variables (study segments). Those dependent variables with the highest correlations with the first canonical variable contributed most to the separation of segments, as the first canonical variable defined the greatest separation of segments (Johnson and Wichern 1992).

The two canonical variables that accounted for most of the separation among study segments were used to form axes. The position of each segment on the two canonical variables was portrayed by plotting study segment scores of

physiochemical categories on the canonical variables and an ellipse was formed around each set of scores for a segment.

For the MANOVA, the null hypothesis tested was the equality of vectors of means of multiple dependent variables (physiochemical variables) across study segments. Klecka (1979) concluded that this multivariate technique is robust enough that the assumptions of a multivariate normal distribution of discriminating variables and equal variance-covariance matrices between groups need not be rigorously met.

Analysis of variance (ANOVA) procedures were used to further interpret the canonical analysis of variates results. Normality and homogeneity of variance were examined prior to the ANOVA. An appropriate transformation, such as arcsine (square root (y)), log (y+1), or square root (y), was applied to dependent variables that violated any of the assumptions (Hair et al. 1995). A one-way ANOVA was performed for each habitat type (main channel and channel border) on each habitat variable (depth, velocity, turbidity, temperature, percent sand, and percent silt) and segment combination.

(3.2) $\quad Y_{ij} = \mu + \alpha_i + \epsilon_{ij}$

$\quad\quad i = 1, 2, \ldots, g$

$\quad\quad j = 1, 2, \ldots, n$

where Y_{ij} = is the jth observation from the ith segment, μ = overall mean (level), α_i = the ith treatment effects (segment), ϵ_{ij} = the error effect associated with Y_{ij} which is normally distributed, g = number of segments, and n = number of observations.

The hypotheses used for ANOVA testing are as follows:

$H_o =$ $\quad \alpha_1 = \alpha_2 = \ldots \alpha_i = 0$ (there is no difference in the habitat characteristics among segments).

$H_A =$ $\quad$ at least one $\alpha_i \neq 0$

A significant F-test for treatments indicated that a physiochemical variable was different among segments, aiding in the interpretation of which physiochemical variables were responsible for segment differences in the canonical analysis. The data were analyzed using the Statistica (Statsoft Inc.1997) software package.

Distribution, Abundance, and Structure

At the time of data collection, the area (m^2) of each habitat type in a sample unit was estimated visually. This information was used to estimate the relative abundance of fish species within each segment. In each year, the catch-per-unit-effort (CPUE; number of fish/m^2) for each species from each habitat type in a sample unit was multiplied times the total area estimated for the habitat in a sample unit, and then summed, yielding an estimate of the number of fish in that sample unit. Total estimated numbers of fish from the sample units were then summed, yielding the total number of fish in the segment for that year. Relative abundance of each species was computed by dividing the total number of estimated fish for a species by the total number of fish estimated for the segment. The relative abundance computed for each species was then averaged across years to obtain the two-year average.

Fish community diversity was examined in each segment by computing measures of species heterogeneity, richness, and evenness. Species heterogeneity in each segment was determined with the reciprocal of Simpson's index (Williams 1964).

(3.3) $D = \sum p_i^2$ (i=1,.....,s fish species)

where D is Simpson's index, p_i is the proportion of fish species i in the community, and $\sum p_i = 1.0$.

Fish species diversity was quantified with the equation:

(3.4)   1/D = fish species diversity

where 1/D is the reciprocal of equation (3.3) which varies from 1 to s, the number of species in the sample.

Species richness was examined with the rarefaction method (Hurlbert 1971, Simberloff 1972). This method was chosen over other richness measures because it corrects for differences in sample size. Species evenness for each segment was computed with Smith and Wilson's index (E) (Smith and Wilson 1996).

(3.5) $E = 1 - [2/\{\pi \text{ arctangent}\{\sum_{i=1}(\log_e(n_i) - \sum_{j=1}(\log_e(n_j)/s)^2/s\}\}]$

where E is Smith and Wilson's index of evenness, n_i is the number of individuals in species i in sample (i=1, 2, 3, 4,......,s), n_j is the number of individuals in species j in sample (j=1, 2, 3, 4,......,s), s is the number of species in the entire sample.

According to Smith and Wilson (1996), this is the best available index of evenness because it is independent of species richness and is sensitive to both rare and common species in the community.

Habitat Use

Habitat where flathead chubs, sicklefin chubs, sturgeon chubs, and western silvery minnows were captured was characterized by graphing the number of samples where each species was present and absent over a range of water depth, velocity, turbidity, and temperature categories and by including the percentage of fish captured in each physiochemical category. This approach depicted which categories for each variable were used most by each species. CPUE was also computed for each species by habitat type and reported by segment.

Predictive Models

Multiple regression models were developed for each species to evaluate fish presence and absence, fish number, and fish density in relation to a variety of environmental variables. Three types of multiple regression models were developed: logistic regression, Poisson regression, and linear regression.

Logistic regression models had fish presence (1) or absence (0) as the dependent variable and turbidity, temperature, substrate expressed as percent sand, percent silt, or percent gravel, discharge, and a principal component of depth and velocity as predictor variables. The relationship between multiple environmental variables and fish presence or absence was described with the logit form of the logistic regression model.

$$(3.6) \quad \text{logit}[\text{pr}(Y=1)] = \beta_0 + \sum_{j=1}\beta_j X_j \qquad (j=1,\ldots\ldots,n \text{ environmental variables})$$

where logit is the transformation of the probability pr(Y=1), β_0 is the y-intercept, β_j is the slope for each environmental variable, and X_j represents the environmental variables.

Models were developed by combining data from all four segments. Predictor variable multicollinearity was examined prior to analysis. Depth and velocity were highly correlated (r>0.90, n=238) therefore, principal component analysis was used to derive a new vector for depth and velocity and used in each logistic regression analysis (Dunteman 1989). Akaike's information criterion (AIC) was computed for all possible combinations of predictor variables (Akaike 1987). The model for each

species with the lowest AIC value was determined to be the one best-fit model. For the one best-fit model for each species, the hat matrix diagonal was used to detect outlier values and Pearson residuals were used to identify observations that were not well explained by the model (Kleinbaum et al. 1998). Final model reliability was examined by using the Chi-square test for covariates which tested whether the variables were statistically significant predictors of fish presence ($P<0.05$ for significance).

Poisson regression had fish counts as the dependent variable and gear effort, current velocity, turbidity, temperature, percent sand or percent gravel, invertebrate drift density, and benthic invertebrate density as predictor variables.

$$(3.7) \quad \log E(Y_i) = \beta_0 + \Sigma_{j=1}\beta_j X_j \quad (j=1,\ldots\ldots,n \text{ environmental variables})$$

where $E(Y_i)$ is the expected number of fish, β_0 is the y-intercept, β_j is the slope for each environmental variable, and X_j represents the environmental variables.

Data from all four segments were combined for model development for sicklefin chub, sturgeon chub, and western silvery minnow. Prior to analysis, predictor variable collinearity was examined with a correlation matrix and multicollinearity was examined by computing variance inflation factor.

A goodness-of-fit statistic, known as deviance (Kleinbaum et al. 1998), derived from maximum likelihood ratios, was used to identify variables that contributed significantly to fish counts (Poisson regression). A forward selection procedure was employed to develop the best-fit model. First, all one-variable models were fit and the model with the smallest deviance was kept. Next, all variables were added one at a time to the best one-variable model to find the two variable model with the lowest deviance. The best two-variable model was compared to a chi-square distribution with 1 degree of freedom. If the chi-square test was significant ($P<0.05$), then the two variable model was retained. All other variables, were added, one at a time to this model until the chi-square test was not significant.

Poisson regression models were developed separately by gear type for fish species. Differences in gear selectivity prevented analysis across gear types. The sicklefin and sturgeon chub Poisson regression models were developed from fish count data obtained from the benthic trawl in main channel habitat. The western

silvery minnow Poisson regression model was developed from fish count data obtained from the bag seine in channel border habitat.

For flathead chub, a linear regression model was developed using CPUE from the bag seine (measured in channel border habitat) as the predictor variable. Linear regression models were not developed for other species because the dependent variable did not approximate a normal distribution. Water velocity, turbidity, temperature, percent sand, invertebrate drift density, and benthic invertebrate density served as predictor variables for CPUE of flathead chub. The relationship between multiple environmental variables and fish CPUE was described with the following form of the multiple regression model.

(3.8) $\quad Y = \beta_0 + \sum_{j=1} \beta_j X_j$ $\qquad$ (j=1,.......,n environmental variables)

where Y is flathead chub CPUE, β_0 is the y-intercept, β_j is the slope for each environmental variable, and X_j represents the environmental variables.

Predictor variable collinearity and multicollinearity were examined in the same manner as for Poisson regression models. Influential observations were identified with Cook's distance. Heteroscedasticity was examined with residual plots and normality of the error term distribution was examined with normal probability plots. The dependent variable was square-root transformed to more closely approximate a normal distribution. AIC was computed for all possible combinations of predictor variables (SAS 1990). The model for each species with the lowest AIC value was determined to be the one best-fit model.

The ability of each best-fit logistic regression model to predict fish presence or absence and the ability of the best-fit Poisson regression models (sicklefin chub and sturgeon chub) to predict fish number was tested against an external data set from the same location. However, before logistic regression model testing could begin, each model's optimum decision rule probability for fish presence or absence was determined. This was accomplished for each best-fit model by plotting decision rule probabilities on the x-axis and the percent of observations classified correctly as present or absent on the y-axis. The decision rule probability with the highest percent of observations classified correctly was considered to be optimum. For the logistic regression models, 60 observations from the external data set were randomly selected that included 30 present and 30 absent observations for a species. The data were entered into each model and a fish was determined to be

present at an observation when the predicted probability was greater than the optimum decision rule probability. Tables depicting the percent correctly and incorrectly classified were developed to examine how well each model predicted fish presence and absence.

For the sicklefin chub and sturgeon chub Poisson regression models, 45 observations where each species was present were randomly selected from the external data set and run through each model. A graph depicting the number of fish predicted by the model on the x-axis and the observed number of fish on the y-axis was generated for each species to examine how well each model predicted fish CPUE. For all regression analyses, the data were analyzed using the Statistical Analysis Systems (SAS 1990) software package.

Habitat Use Distinctiveness

The procedure used to examine distinctiveness of habitats among segments (MANOVA and canonical analysis of variates) was also used to examine the distinctiveness of habitat use by each of the four cyprinid species. The MANOVA was conducted across presence/absence categories for each species, with presence or absence serving as the independent variable and environmental variable categories serving as the dependent variables (these variables were depth/velocity principal component, turbidity, temperature, percent silt, percent sand, invertebrate drift, and discharge).

$$(3.9) \quad Y_{ir} = \mu + T_i + e_{ir}$$

$$i = 1, 2$$

$$r = 1, 2, \ldots, n$$

where Y_{ir} = the environmental variable (r) value for presence/absence category i, μ = overall mean (level), T_i = the ith treatment effects (fish presence or absence), e_{ir} are independent, normally distributed variables, and n = number of environmental variables.

The hypotheses used for MANOVA testing are as follows:

$H_o=$ $T_1 = T_2 = 0$ (there is no difference in habitats where fish were present or absent).

$H_A=$ at least one $T_i \neq 0$

Assumptions for the MANOVA were examined with procedures identical to those employed in the habitat distinctiveness analysis. Interpretation of the MANOVA and canonical analysis of variates also follows that described for the habitat distinctiveness analysis. An appropriate transformation, such as arcsine (square root (y)), log (y+1), or square root (y), was applied to dependent variables that violated any of the assumptions (Hair et al. 1995).

Analysis of variance (ANOVA) procedures were also used to further interpret the canonical analysis of variates results. Normality and homogeneity of variance were examined prior to ANOVA. A one-way ANOVA was performed for each habitat variable (depth, velocity, turbidity, temperature, percent sand, percent silt, invertebrate drift, and discharge) and fish species catch combination. The fish catch variable was presence (1) or absence (0).

(3.10) $Y_{ij} = \mu + \alpha_i + \epsilon_{ij}$

$i = 1, 2$

$j = 1, 2, \ldots, n$

where Y_{ij} = is the jth observation from the ith presence/absence category, μ = overall mean (level), α_i = the ith treatment effects (presence or absence), ϵ_{ij} = the error effect associated with Y_{ij} which is normally distributed, i = presence or absence categories, and n = number of observations.

The hypotheses used for ANOVA testing are as follows:

H_o= $\alpha_1 = \alpha_2 = 0$ (there is no difference in the habitat characteristics among segments).

H_A= at least one $\alpha_i \neq 0$

A significant F-test for treatments indicated that the water physiochemical variable is different among presence and absence catch locations, aiding in the interpretation of which environmental variables are responsible for presence/absence differences in the canonical analysis. An appropriate transformation, such as arcsine (square root (y)), log (y+1), or square root (y), was applied to dependent variables that violated any of the assumptions (Hair et al. 1995). The data were analyzed using the Statistica (Statsoft Inc.1997) software package.

Habitat-Niche Distinctiveness

Distinctiveness of the habitat niche within the family Cyprinidae was examined for the four species that were captured frequently enough for analysis: flathead chub, sicklefin chub, sturgeon chub, and western silvery minnow. The procedure used to examine distinctiveness of habitats among segments and distinctiveness of habitat use by each of the four cyprinid species (MANOVA + canonical analysis of variates) was also used to examine habitat-niche relations. Multivariate analysis of variance (MANOVA; Johnson and Wichern 1992) was conducted across species from the four study regions, with cyprinid species and years serving as the independent variables and water physiochemical categories serving as the dependent variable (depth, velocity, turbidity, temperature, percent silt, percent sand).

$$(3.11)\ Y_{rij} = \mu + T_i + \beta_j + y_{ij} + e_{ijr}$$

$$i = 1, 2, \ldots\ldots, g$$

$$j = 1, 2$$

$$r = 1, 2, \ldots\ldots, n$$

where Y_{rij} = is the rth physiochemical variable value for species i in year j, μ = overall mean (level), T_i = species i effect, β_j = the year j effect, y_{ij} = interaction between species and years, e_{ijr} are independent, normally distributed variables, g = number of fish species, and n = number of physiochemical categories.

The hypotheses used for MANOVA testing are as follows:

$H_o=$ $T_1 = T_2 = \ldots..T_g = 0$ (there is no difference in habitat use among cyprinid species).

$H_A=$ at least one $T_i \ne 0$

Assumptions for the MANOVA were examined with procedures identical to those employed in the habitat distinctiveness analysis. Interpretation of the MANOVA and canonical analysis of variates also follows that described for the habitat distinctiveness analysis. Analysis of variance (ANOVA) procedures were also used to further interpret the canonical analysis of variates results. A one-way ANOVA was performed for each physiochemical category (depth, velocity, turbidity, temperature, percent sand, percent silt) with fish species serving as treatments.

$$(3.12) \; Y_{ij} = \mu + \alpha_j + e_{ij}$$

$$i = 1, 2, \ldots, g$$

$$j = 1, 2, \ldots, n_i$$

where Y_{ij} = is the jth observation for the ith species, μ = overall mean (level), α_i = species i effect, e_{ij} = the error effect associated with Y_{ij} that is normally distributed, g = number of species, j = number of observations, and n_i = number of observations of species i.

The hypotheses used for ANOVA testing are as follows:

H_o= $\quad \alpha_1 = \alpha_2 = \ldots \alpha_g = 0$ (there is no difference in the use of the physiochemical variable among fish species).

H_A= $\quad$ at least one $\alpha_g \neq 0$

A significant F-test for treatments indicated that the water physiochemical category was used differently by the four fish species, aiding in the interpretation of which physiochemical variables are responsible for habitat use differences in the canonical analysis. An appropriate transformation, such as arcsine (square root (y)), log (y+1), or square root (y), was applied to dependent variables that violated any of the assumptions (Hair et al. 1995). The data were analyzed using the Statistica (Statsoft Inc.1997) software package.

RESULTS

Distribution, Abundance, and Structure

A total of 3,302 fish representing 28 species (Tables 3.1-3.4) was sampled from the four study segments: 265 from the ACS (214 channel border, 51 main channel), 1,241 from the BCS (1,166 channel border, 76 main channel), 356 from the MZS (356 channel border, 75 main channel), and 1,095 from the YRS (891 from channel border, 204 from main channel).

Flathead Chub

Flathead chub was the most abundant species in each of the four segments (1,611 fish) representing from 33% (MZS) to 65% (BCS) of the catch in any one segment (Tables 3.1-3.4). Approximately 99% of flathead chubs sampled in the four

segments were captured with the bag seine. Most flathead chubs in all study segments ranged from 20-40 mm in length (Figure 3.3). The BCS and YRS had high proportions of flathead chub less than 50 mm in length.

Sicklefin Chub

The greatest number of sicklefin chubs was captured in the BCS (49 fish). This species had its highest relative abundance, however, in the ACS (9.8%) (Tables 3.1-3.4). Ninety-two percent of all sicklefin chubs were captured with the trawl. Sicklefin chubs ranged from 30 mm to 120 mm in length (Figure 3.4). Most fish ranged from 60 to 90 mm in length with chubs less than 40 mm found in the BCS, the MZS, and the YRS. No sicklefin chubs less than 60 mm were captured in the ACS.

Sturgeon Chub

The highest relative abundance of sturgeon chubs was found in the YRS (12.1%) where the greatest number of this species was also captured (92) (Tables 3.1-3.4). Eighty-five percent of all sturgeon chubs were captured with the trawl. Sturgeon chubs ranged from 20-80 mm in length (Figure 3.5). Length-frequency distributions were irregular with year classes missing in the ACS, BCS, and MZS. Fish less than 40 mm were captured in all study segments, with the highest proportion in the YRS.

Western Silvery Minnow

The greatest number of western silvery minnows was captured in the BCS (169 fish); this segment also had the highest relative abundance of the species (9.8%) (Tables 3.1-3.4). More than over 98% of all western silvery minnows were captured with the bag seine. Western silvery minnows ranged from 13 mm to 96 mm in length in the four segments (Figure 3.6). Length-frequency distributions were irregular in all study segments with year classes missing. Both the BCS and the YRS had high proportions of fish less than 35 mm.

Species Diversity, Evenness, and Richness

The MZS exhibited the highest species diversity (1/D=6.48, equation 3.4) and the highest species richness (18.23) (Table 3.5). The highest species evenness was found in the ACS (E=0.32, equation 3.5). The lowest species diversity was

found in the BCS (1/D=2.14), whereas the lowest species richness (11.82) and evenness (E=0.16) were found in the YRS.

Habitat Use

In the four segments, 99% of the 1611 flathead chubs were captured in the shallow, channel border habitat (Tables 3.1-3.4). In this habitat, the highest CPUE for flathead chub was in the BCS (20.4 fish/m^2) and the lowest in the MZS (4.1 fish/m^2) (Table 3.6). CPUE of flathead chubs was low (<0.1 fish/ 100 m^2) in main channel habitat in all four segments.

Ninety-seven percent of the 147 sicklefin chubs were captured in the deep, high velocity main channel habitat in the four study segments (Tables 3.1-3.4). The highest CPUE found for sicklefin chub in this habitat was in the YRS (0.4 fish/ 100 m^2) and the lowest in the ACS and MZS (0.2 fish/ 100 m^2) (Table 3.6). Sicklefin chubs were not captured in the shallow, channel border habitat except for four fish (3%) in the BCS.

Most of the 155 sturgeon chubs were captured in main channel habitat (85%) (Tables 3.1-3.4). In this habitat, the highest CPUE for sturgeon chub was found in the YRS (0.7 fish/100 m^2) and the lowest in the MZS (<0.1 fish/100 m^2) (Table 3.6). CPUE was low for sturgeon chub in channel border habitat in all four segments, but was highest in the YRS (0.3 fish/m^2).

Most western silvery minnows were captured in channel border (98%) (Tables 3.1-3.4). In channel border, the BCS had the highest CPUE for western silvery minnow (4.4 fish/m^2) and the ACS had the lowest CPUE (0.6 fish/m^2) (Table 3.6). Few western silvery minnows were captured in the main channel.

Overall, the highest catch rates for sicklefin chub, sturgeon chub, western silvery minnow, and flathead chub were found in BCS and YRS. Catch rates for these species were similar in the ACS and MZS. Catch rates for other fish species varied among the segments (Table 3.6).

Nearly all fish collection samples taken at sites less than 1 m in depth (93%) and 0.25 m/sec in velocity (94%) contained flathead chubs (Figure 3.7). More than 99% of flathead chub were captured in depths less than 1 m and 90% were captured in current velocity less than 0.25 m/sec. Sixty-six percent of flathead chub were captured in turbidities less than 250 NTU. Sixty-two percent of flathead chub were captured in temperatures between 18-22 °C. (Figure 3.7).

Few samples taken at depths less than 2 m or velocities less than 0.5 m/sec contained sicklefin chubs (Figure 3.8). Approximately 86% and 64% of sicklefin chub were captured in depths from 2-5 m and in current velocity from 0.5-1.0 m/sec, respectively. Most sicklefin chubs were captured in turbidities less than 500 NTU (87%) and in temperatures between 20-24 °C (83%) (Figure 3.8).

Sturgeon chub were captured in samples taken at all depth and nearly all current velocity categories (Figure 3.9). The highest proportion of samples containing fish were from 2-4 m in depth and exhibited 0.5-1 m/sec current velocities. Approximately 88% and 81% of sturgeon chub were captured in depths from 2-5 m and in current velocities from 0.5-1 m/sec. Few samples with turbidities greater than 500 NTU or with temperatures less than 18 °C or greater than 24°C contained sturgeon chub (Figure 3.9). Most sturgeon chub were captured in turbidities less than 250 NTU (78%) and in temperatures between 18-22 °C (80%).

Ninety-eight percent of western silvery minnows were captured in depths less than 1 m and in current velocity less than 0.5 m/sec (Figure 3.10). Most western silvery minnows were captured in turbidities less than 250 NTU (85%) and in temperatures between 18-22 °C (64%).

Segment and Habitat Characterization

The two segments that were most physiochemically similar were the YRS and MZS, with the ACS the most dissimilar (Figure 3.11). Among the segments, channel border habitat was similar in depth, current velocity, and turbidity (Table 3.7). The mean water temperature was nearly 2 °C cooler in the ACS and both the ACS and the MZS contained twice the mean percent composition of silt as compared to the other two study segments. Current velocity and substrate composition were similar among the four study segments in main channel habitat (Table 3.8). Mean depth (5.4 m) and turbidity (239.4 NTU) were greater in the MZS than the other three study segments. Mean water temperature was lowest in the ACS (19.0 °C) and highest in the YRS (21.6 °C).

Significant differences in physiochemical characteristics were found among segments in both habitat types (main channel, MANOVA, Wilk's Lambda=0.5641, $P<0.0001$; channel border, MANOVA, Wilk's Lambda=0.6324, $P<0.001$), but not years (main channel, MANOVA, Wilk's Lambda=0.2142, $P=0.71$; channel border, MANOVA, Wilk's Lambda=0.2334, $P=0.11$). No significant interaction was found

between study segments and years for either main channel habitat (MANOVA, Wilk's Lambda=0.1764, P=0.22) or channel border habitat (MANOVA, Wilk's Lambda=0.2875, P=0.09).

The canonical analysis of water physiochemical data from main channel habitat derived three canonical variables, each a composite of the six physiochemical variables retained (Table 3.9). The first two canonical variables accounted for approximately 80% of the physiochemical differences among the four segments. Depth exhibited the largest score (standardized canonical coefficient) on the first canonical variable (depth=-0.9808) which indicates that this variable was responsible for most of the habitat physiochemical differences among the four segments.

For main channel habitat, plots of individual scores on the first two canonical variables revealed three groups (Figure 3.12). One group consisted of the YRS and MZS, the second group included the BCS, and the third group included the ACS. The YRS and MZS showed nearly complete overlap. The ACS and BCS were separated from the other two segments on the horizontal axis by depth and from these two segments and each other on the vertical axis by velocity (Figure 3.12).

The canonical analysis of water physiochemical data from channel border habitat derived three canonical variables, each a composite of the six physiochemical variables retained (Table 3.10). The first two canonical variables accounted for approximately 85% of the physiochemical differences among the four segments. Depth exhibited the largest score (standardized canonical coefficients) on the first canonical variable (depth=0.8003) which indicates that this variable was responsible for most of the habitat physiochemical differences among the four segments.

For channel border habitat, plots of individual scores on the first two canonical variables revealed that the four segments overlapped with one another to varying degrees (Figure 3.13). The YRS exhibited a high degree of overlap with both the BCS and MZS. The ACS and the YRS showed separation only on the vertical axis by substrate, whereas the BCS and MZS only showed separation on the horizontal axis by depth (Figure 3.13).

Different physiochemical variables in main channel habitat and in channel border habitat were responsible for differences among segments. For main channel

habitat, depth (ANOVA, F=11.33, $P<0.0001$), velocity (ANOVA, F=7.64, $P<0.0001$), turbidity (ANOVA, F=2.92, $P=0.04$), and temperature (ANOVA, F=8.60, $P=0.0001$) differed significantly among segments (Table 3.10). For channel border habitat, depth (ANOVA, F=4.16, $P=0.0087$) was also significant. Percent silt (ANOVA, F=4.31, $P=0.0073$) and percent sand (ANOVA, F=3.79, $P=0.01$) were also significantly different among segments (Table 3.10).

Habitat Use Distinctiveness

Significant differences were found between the habitats where fish were present and absent for flathead chub (MANOVA, Wilk's Lambda=, $P<0.0001$), sicklefin chub (MANOVA, Wilk's Lambda=0.000, $P<0.0001$), sturgeon chub (MANOVA, Wilk's Lambda=0.8666, $P<0.0001$), and western silvery minnow (MANOVA, Wilk's Lambda=0.7747, $P<0.0001$). Therefore, I rejected the null hypothesis that there was no difference in habitat characteristics where any of the four minnow species were present or absent.

For each species, canonical analysis of habitat data from minnow collection sites derived a single variable, each a composite of the six environmental variables retained (Table 3.11). For each species, the original variables with the largest scores (standardized canonical coefficients) on the canonical variable were: flathead chub - depth/velocity principal component (-0.9283); sicklefin chub - silt (1.0382); sturgeon chub - silt (-1.0895); western silvery minnow - depth/velocity principal component (-0.9782). Since the canonical variable gives the greatest separation among the sample sites based on the habitat data, the environmental categories that exhibit the highest correlation with the canonical variable drives this separation. For each of the four species, the environmental variables listed above are responsible for most of the variation in habitat use.

Significant differences were also found between the habitat characteristics of minnow sampling sites (Table 3.11). For flathead chub and western silvery minnow, depth and velocity (flathead chub, ANOVA, F=1.61, $P<0.0001$; western silvery minnow, ANOVA, F=6.48, $P<0.0001$) percent silt (flathead chub, ANOVA, F=6.47, $P<0.0001$; western silvery minnow, ANOVA, F=27.01, $P<0.0001$), and percent sand (flathead chub, ANOVA, F=1.61, $P<0.0001$; western silvery minnow, ANOVA, F=21.97, $P<0.0001$) differed between sample sites where fish were present or absent (Table 3.11). Depth and velocity (ANOVA, F=11.85, $P=0.0007$), temperature (ANOVA, F=5.81, $P=0.02$), percent silt (ANOVA, F=19.57, $P<0.0001$), percent sand

(ANOVA, F=14.06, P=0.0002), and discharge (ANOVA, F=9.49, P=0.0023) differed significantly between sampling sites where sicklefin chub were present and absent (Table 3.11). For sturgeon chub, percent silt (ANOVA, F=4.49, P=0.04) and discharge (ANOVA, F=25.74, P<0.0001) differed between sample sites where fish were present or absent (Table 3.11).

Predictive Models

For flathead chub, sicklefin chub, sturgeon chub, and western silvery minnow, I I rejected the null hypothesis that there was no difference in habitat characteristics where fish were sampled and not sampled. For flathead chub, one variable, the principal component of depth and velocity, was significantly (multiple logistic regression; P<0.0001) related to flathead chub presence (1) or absence (0) (Table 3.12). Based on the odds ratio, a 1 m decrease in depth and a decrease of 1 m/sec in current velocity would increase the odds of a flathead chub being present by 4 times.

For sicklefin chub, four variables--temperature, percent sand, discharge, and the depth/velocity principal component were significantly (multiple logistic regression; P<0.0001) related to sicklefin chub presence (1) or absence (0) (Table 3.12). Based on the odds ratio, if all other variables were held constant, an increase in depth of 1 m and an increase in velocity of 1 m/sec would increase the odds of a sicklefin chub being present by 3.1 times. For water temperature, an increase of 2 °C would increase the odds of there being a sicklefin chub present by 1.6 times. For sand and discharge, an increase in percent sand of 50% and a decrease in discharge by 300 m³/sec leads to an increase in the odds of a sicklefin chub being present by 1.8 and 2.5 times, respectively.

For sturgeon chub, two variables, percent sand and discharge were significantly (multiple logistic regression; P<0.0001) related to sturgeon chub presence (1) or absence (0) (Table 3.12). Based on the odds ratio, if all other variables were held constant, a 50% increase in sand would increase the odds of there being a sturgeon chub present by 1.2 times. For discharge, a decrease of 300 m³/sec would increase the odds of there being a sturgeon chub present by 1.8 times.

For western silvery minnow, two variables, the depth/velocity principal component and percent sand were significantly (multiple logistic regression;

P<0.0001) related to presence (1) or absence (0) (Table 3.12). Based on the odds ratio, if all other variables were held constant, a decrease of 1 m in depth and a decrease of 1 m/sec in velocity would increase the odds of a western silvery minnow being present by 1.2 times. For sand, an increase of 50 percent would increase the odds of there being a western silvery minnow present by 2.0 times.

For sicklefin chub, sturgeon chub, and western silvery minnow, I rejected the null hypotheses that there was no difference in habitat characteristics based on fish number. For the sicklefin chub, two variables, current velocity and temperature were significantly (multiple Poisson regression; *P*<0.0001, R^2=0.32) related to sicklefin chub number (Table 3.12). Based on the predicted number of fish, if all other variables were held constant, a 0.25 m/sec decrease in current velocity would increase the number of fish by 1.8 times. For temperature, an increase of 2 °C would increase the number of fish by 1.2 times.

For sturgeon chub, four variables, discharge, percent gravel, current velocity, and turbidity were significantly (multiple Poisson regression; *P*<0.0001, R^2=0.55) related to fish number (Table 3.12). If all other variables were held constant, decreasing the discharge by 500 m^3/sec, the current velocity by 0.50 m/sec, and the turbidity by 250 NTU the number of sturgeon chub would increase by 1.0, 3.6, and 1.0 times, respectively. An increase of 50% in gravel would increase the number of fish by 1.2 times.

For western silvery minnow, four variables, effort, current velocity, percent sand, and benthic invertebrate density were significantly (multiple Poisson regression; *P*<0.0001, R^2=0.43) related to fish number (Table 3.12). Based on the predicted number of fish, if all other variables were held constant, a decrease in current velocity of 0.25 m/sec and an increase in fish gear effort of 10 m^2 would increase the number of fish by 31.2 and 1.1 times, respectively. Similarly, an increase in sand by 50% and in benthic invertebrate density by 100 organisms/m^2 would increase the number of fish by 1.0 and 1.2 times, respectively.

For flathead chub, I rejected the null hypothesis that there was no difference in habitat characteristics based on fish CPUE (number fish/m^2). Four variables, current velocity, turbidity, percent sand, and benthic invertebrate density were significantly (multiple linear least-squares regression; *P*<0.0001, R^2=0.47) related to flathead chub CPUE (Table 3.12). Based on fish CPUE, if all other variables were held constant, a decrease in current velocity of 0.25 m/sec would increase flathead

chub CPUE by 1.4 times. Similarly, an increase in sand by 50%, an increase in turbidity by 500 NTU, and an increase in benthic invertebrate density by 100 organisms/m² would increase the CPUE by 2.0 times each.

For logistic regression model testing, optimum decision rule probabilities ranged from 0.50 for sicklefin chub to 0.65 for flathead chub (Figure 3.14). The flathead chub logistic model worked best, predicting flathead chub presence correctly at a rate of 90% and predicting both flathead chub presence and absence at a rate of 95% (Table 3.13). The logistic models developed for western silvery minnow and sicklefin chub also performed well. Western silvery minnow presence and combined presence and absence was predicted correctly at rates of 97% and 80%, respectively (Table 3.13). Sicklefin chub presence was predicted correctly at a rate of 70% whereas, combined presence and absence was predicted correctly 80% of the time. The logistic model developed for sturgeon chub performed poorest. It correctly predicted chub presence and combined presence and absence only 57% and 55% of the time, respectively (Table 3.13).

The sicklefin chub and sturgeon chub Poisson models also showed close agreement between the number of fish observed and the number of fish predicted by both models (sicklefin chub, r=0.45, Figure 3.15; sturgeon chub, r=0.52, Figure 3.16).

Habitat Niche Distinctiveness

Habitat use among flathead chub, sicklefin chub, sturgeon chub, and western silvery minnow differed (MANOVA, Wilk's Lambda=0.4357, $P<0.001$). No difference in habitat use was found among years, however (MANOVA, Wilk's Lambda=1.5644, $P=0.10$). No significant interaction was found between species and years (MANOVA, Wilk's Lambda=1.7801, $P=0.40$). The canonical analysis of habitat use data derived three canonical variables, each a composite of the six physiochemical variables retained (Table 3.14). The first two canonical variables accounted for approximately 99% of the habitat use differences among the four species. Current velocity and temperature exhibited the largest scores (standardized canonical coefficients) on the first canonical variable (current velocity, -0.6854; temperature, 0.6362) which indicates that these two physiochemical variables were responsible for most of the habitat use differences among the four species in the segments (Table 3.14).

Plots of individual scores on the first two canonical variables revealed two groups of species among the four groups of species investigated that exhibited high niche overlap (Figure 3.17). One group consisted of flathead chub and western silvery minnow; these two species were nearly identical in their use of low current velocity habitat. The second group included the sicklefin and sturgeon chubs, which overlapped in use of habitats with high current velocity. Sturgeon chub also overlapped with western silvery minnow and flathead chub in use of lower current velocity habitat. Little separation in use was detected among the four species with regard to temperature however, sicklefin chubs used main channel habitat almost exclusively, resulting in less overlap with flathead chubs and western silvery minnows.

Significant differences were also found among the four species' habitat use using ANOVA (Table 3.14). Depth (ANOVA, F=64.69, P<0.0001), velocity (ANOVA, F=84.09, P<0.0001), percent silt (ANOVA, F=28.10, P<0.0001) and percent sand (ANOVA, F=12.72, P<0.0001) use differed significantly among the four species (Table 3.14).

DISCUSSION

Segment and Habitat Characterization

The physiochemical differences among the study segments indicated the presence of distinctly different habitat conditions for fishes among study segments, especially between the ACS and the other segments. For example, the YRS was characterized by high turbidity, high summer water temperatures (in the main channel), and high discharge. In comparison, the ACS of river exhibited lower main channel turbidity, lower water temperature (as compared to the other study segments), and lower discharge. Many of the differences are a result of the strong influence of the Yellowstone River on downstream segments and the influence of Fort Peck dam on the ACS. Fort Peck dam acts as a sediment sink, trapping inflowing suspended sediment, and limiting downstream movement of the river's suspended load (Leopold 1964). As a result, turbidity is reduced in the ACS. Hypolimnetic withdrawals from Fort Peck Dam also have reduced the summer water temperatures in the ACS. Peak water temperatures in the ACS were from 4.9 to 6.1

°C cooler than the other segments (Table 3.8). The influence of the Missouri River above the confluence on the physiochemical characteristics of the MZS and BCS was dampened by the higher discharge exhibited by the Yellowstone River for most of the study period (July-September) in both 1997 and 1998 (Figure 3.18), causing the ACS to be greatly different from the other segments.

Habitat Use

Flathead chub and western silvery minnow used similar depths, velocities, turbidities, temperatures, and substrates. I found that in samples containing western silvery minnows, flathead chubs were also present 83% of the time and in samples containing flathead chubs, western silvery minnows were present approximately 40% of the time. Gould (1985) also frequently captured these two species together in the Musselshell River, Montana. In this study, both species commonly used depths less than 1 m and current velocities less than 0.25 m/sec, with few individuals of either species captured in the deeper, swifter main channel. Habitat models for both species also included depth and velocity as significant variables in predicting fish presence or abundance, with decreasing depth and velocity resulting in increasing fish number or presence probability. Similarly, canonical analysis of physiochemical data measured at sampling sites revealed that depth and velocity strongly influenced where these two species were present and absent.

Pflieger and Grace (1987) documented the precipitous decline in both flathead chub and western silvery minnow in the lower Missouri River over a 40 year period. They hypothesized that the decline in flathead chub was related to reduced turbidity and competition with other fish species and the reduction in western silvery minnow was due to reduced sediment transport and loss of silty backwater habitat. Results of this study indicate that shallow, low velocity habitat is important for flathead chub. The near absence of this habitat in the lower Missouri River may also be a contributing factor responsible for both species' decline there.

Sicklefin chub, in contrast, were more associated with the main channel. They commonly used sand substrate and depths greater than 3 m and current velocities greater than 0.5 m/sec. Grisak (1996) found that sample sites containing this species averaged 0.58 m/sec current velocity, 3.4 m depth, and 70% sand substrate. In this study, the mean depth occupied was similar (3.7 m) as in his study. Sites where chubs were found in the present study contained 1.3 times more

sand (90.8%) and exhibited an average current velocity (0.9 m/sec) that was 1.6 times swifter than sites in Grisak's (1996) study. Habitat models predicting either presence or abundance for this species included percent sand, current velocity, and discharge as significant variables, with an increase in percent sand and current velocity and a decrease in discharge positively influencing fish presence or abundance. Similar results were obtained by Everett (1999) for sicklefin chub in the confluence area in 1995. The influence of discharge on fish presence or abundance must be its effect on trawl CPUE. For sicklefin chub (r=-0.30), discharge and CPUE are negatively correlated. Perhaps at high discharge, a greater amount of suitable habitat is available, thereby reducing fish density and negatively affecting CPUE.

Sturgeon chub commonly used sand substrate and depths ranging from 0 to 4 m and current velocities ranging from 0 to 1.0 m/sec. Habitat models for this species included percent gravel, current velocity, and discharge as significant variables in predicting fish abundance, with an increase in percent gravel and a decrease in current velocity and discharge positively influencing fish number. Everett (1999) also found that a decrease in current velocity positively influenced the presence of sturgeon chub. Other researchers found that gravel was the primary substrate used by sturgeon chub (Davis and Miller 1967, Baxter and Simon 1970, Elser et al. 1980, Burr and Warren 1986, Gould 1994, Gelwicks et al. 1996). I found the primary substrate used by sturgeon chub was sand. Increasing percent gravel at sample sites positively influenced sturgeon chub density, however. The negative influence (r=-0.34) of discharge on CPUE is similar to that observed for sicklefin chub.

Habitat Niche Distinctiveness

Niche overlap analysis has been used as an indicator of the possible importance of competition in shaping resource use in communities (McNeely 1982). However, it has also been used to examine niche segregation in species resource use (Desselle et al. 1978). In this study, habitat niche segregation was found among the four species to varying degrees. Canonical analysis indicated that the primary difference in habitat use among the four species was due to current velocity. Western silvery minnow and flathead chub overlapped to a high degree in their use of water with low current velocities. The common occurrence of flathead chub and western silvery minnow in samples elsewhere (Gould 1985, Pflieger 1975) indicates that these two species overlap in their resource use at other locations. Flathead

chub and *Hybognathus spp.* have also been found to overlap in habitat use with sturgeon chub (Gould 1994) which is similar to results found in this study.

Sicklefin chub and sturgeon chub exhibited high overlap in their use of high current velocity habitat, but sturgeon chub also exhibited use of low current velocity habitat whereas sicklefin chub did not. Similarly, Everett (1999) found that even though sicklefin and sturgeon chubs were frequently captured together in habitats with high current velocity, sturgeon chub were found in additional habitats exhibiting very low current velocities.

Distribution, Abundance, Density, and Structure

The higher density, catch, and abundance for flathead chub and western silvery minnow in the YRS and BCS, in addition to the more uniform length-frequency distributions, indicates that these two segments are better habitat for these species of fish than the ACS and MZS of river. Most individuals of both species were captured in channel border habitat in all four study segments. This habitat exhibited lower current velocities and a greater percentage of sand substrate in the YRS and BCS than in the ACS and MZS. Habitat models predicting fish abundance and density included both these variables, with abundance of both species increasing as velocity decreased and percent sand increased.

The YRS and BCS main channel habitats yielded the highest densities and catches of sicklefin chubs indicating that these two segments were better habitat for this species than the ACS and MZS. A habitat model using sicklefin chub abundance data from this habitat included current velocity and temperature, with abundance of sicklefin chubs increasing as velocity increased and temperature increased. Approximately 72% of sicklefin chub were captured in current velocities between 0.75 and 1.25 m/sec. High proportions of trawl subsamples in both the YRS (86%) and BCS (77%) fell within this velocity category; lower proportions of trawl subsamples in the ACS (62%) and MZS (56%) were within this range of current velocity. Similarly, water temperatures were highest in main channel habitat in the YRS, where this species achieved its highest CPUE.

The higher density, catch, and abundance for sturgeon chub in the YRS and BCS, in addition to the more uniform length-frequency distributions, indicated that these two segments were better habitat for this species than the ACS and MZS of river. Most sturgeon chub samples were collected in August and September of

1998 in main channel habitat within the YRS. At this time, the river discharge was lower in the YRS than in the other three segments, which explains the inclusion of this variable in both sturgeon chub models. Coarser substrates (more sand and gravel) were found in both habitat types in YRS and BCS than in the other two segments. The habitat models predicting fish presence and fish number included both these variables, with the presence of sturgeon chub increasing with decreasing discharge and increasing coarseness of substrate.

The importance of the mixing zone to native species of fish was difficult to ascertain. This segment had high catch rates for sicklefin chub and western silvery minnow and exhibited the highest catch rates for shovelnose sturgeon (*Scaphirhynchus platorynchus*), goldeye (*Hiodon alosoides*), river carpsucker (*Carpiodes carpio*), age-0 sauger (*Stizostedion canadense*), and age-0 walleye (*Stizostedion vitreum*), all native species of fish. A single pallid sturgeon (*Scaphirhynchus albus)* approximately 1000 mm in length and 22-28 kg in weight, a federally endangered species, was also captured in the MZS with the trawl. Pallid sturgeon also have been frequently captured in this segment in the past (Steve Krentz, United States Fish and Wildlife Service, Bismarck, North Dakota, Personal Communication) indicating that it may be important habitat for this species.

At this time, the status of flathead chub, sicklefin chub, sturgeon chub, and western silvery minnow is a subject of debate. In the lower Missouri River, the abundance of these four species has declined precipitously since the onset of dam construction and channelization (Pflieger and Grace 1987) and each has received considerable support for listing under the Endangered Species Act (Werdon 1993a, 1993b; Hesse 1994). However, studies conducted in the upper Missouri and lower Yellowstone Rivers (Gould 1994, Grisak 1996, Young et al. 1997, Everett 1999) suggest that the status of these species may be less a cause for concern in Montana and North Dakota, based on their widespread distribution and abundance. In this study, these four species made up over 65% of the catch, indicating that their status is better in the confluence area than in many portions of the middle and lower Missouri Rivers.

For sustainable populations of flathead chub, sicklefin chub, sturgeon chub, and western silvery minnow in the upper Missouri and lower Yellowstone Rivers, natural river characteristics, such as a naturally fluctuating hydrograph and a high sediment load, that produce a diversity of habitats and habitat conditions should be

preserved, and if possible, improved in altered river segments. Channel modifications, such as bank stabilization and additional irrigation withdrawals, that would alter natural river habitat should be discouraged.

LITERATURE CITED

Akaike, H. 1987. Factor analysis and AIC. Psychometrika 52: 317-332.

Bain, M. B. 1985. Fish community structure in rivers with natural and modified daily flow regimes. Doctoral dissertation. University of Massachusetts, Amherst.

Barila, T. Y., R. D. Williams, and J. R. Stauffer, Jr. 1981. The influence of stream order and selected stream bed parameters on fish diversity in Raystown Branch, Susquehanna River drainage, Pennsylvania. Journal of Applied Ecology 49: 193-198.

Baxter, G. T., and J. R. Simon. 1970. Wyoming fishes. Wyoming Game and Fish Department, Bulletin 4, Cheyenne.

Box, G. E. P. 1949. A general distribution theory for a class of likelihood criteria. Biometrika 36: 317-346.

Burr, B. M., and M. L. Warren, Jr. 1986. A distributional atlas of Kentucky fishes. Kentucky Nature Preserve Commission, Scientific and Technical Series, No. 4, Frankfort.

Davis, B. J., and R. J. Miller. 1967. Brain patterns in minnow of the genus *Hybopsis* in relation to feeding habits and habitat. Copeia 1967: 1-39.

Desselle, W. J., M. A. Poirrier, J. S. Rogers, and R. C. Cashner. 1978. A discriminant functions analysis of sunfish (*Lepomis*) food habits and feeding niche segregation in the Lake Pontchartrain, Louisiana Estuary. Transactions of the American Fisheries Society 107: 713-719.

Dunteman, G. H. 1989. Principal components analysis. Sage Publications: Quantitative applications in the Social Sciences, Series number 07-069. Sage Publications, Thousand Oaks, California.

Duque, A. B., D. C. Taphorn, and K. O. Winemiller. 1998. Ecology of the coporo, *Prochilodus mariae* (Characiformes, Prochilodontidae), and status of annual migrations in western Venezuela. Environmental Biology of Fishes 53: 33-46.

Elser, A. A., M. W. Gorges, and L. M. Morris. 1980. Distribution of fishes in southeast Montana. Montana Department of Fish, Wildlife, and Parks, Miles City.

Everett, S. R. 1999. Ecology and life history of three native benthic fishes in the Missouri and Yellowstone River. Master's thesis. University of Idaho, Moscow.

Gehrke, P. C., K. L. Astles, and J. H. Harris. 1999. Within-catchment effects of flow alteration on fish assemblages in the Hawkesbury-Nepean River System, Australia. Regulated Rivers: Research and Management 15: 181-198.

Gelwicks, G. T., K. Graham, D. Galat, and G. D. Novinger. 1996. Status survey for sicklefin chub, sturgeon chub, and flathead chub in the Missouri River, Missouri. Final Report. Missouri Department of Conservation, Columbia.

Gould, W. 1985. Aspects of the biology of the flathead chub (*Hybopsis gracilis*) in Montana. Great Basin Naturalist 45(2): 332-336.

Gould, W. R. 1994. The recent distribution of sturgeon chub (*Macrhybopsis gelida*) in Montana. Unpublished Report, Montana State University, Bozeman.

Grisak, G. G. 1994. Sicklefin project summary. Montana Department of Fish, Wildlife, and Parks, Lewistown.

Grisak, G. G. 1996. The status and distribution of the sicklefin chub in the middle Missouri River, Montana. Master's thesis. Montana State University, Bozeman.

Hair, J. F., Jr., R. E. Anderson, R. L. Tatham, and W. C. Black. 1995. Multivariate data analysis with readings. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.

Hesse, L. W., J. C. Schmulbach, J. M. Carr, K. D. Keenlyne, D. G. Unkenholz, J. W. Robinson, and G. E. Mestl. 1989. Missouri River fishery resources in relation to past, present, and future stresses. Pages 352-371 *in* D. P. Dodge, editor. Proceedings of the International Large River Symposium. Canadian Special Publications of Fisheries and Aquatic Science, 106, Ottawa, Ontario, Canada.

Hesse, L. W. 1994. The status of Nebraska fished in the Missouri River, 5. Selected chubs and minnows (Cyprinidae): Sicklefin chub (*Macrhybopsis meeki*), sturgeon chub (*M. gelida*), silver chub (*M. storeriana*), speckled chub (*M. aestivalis*), flathead chub (*Platygobio gracilis*), plains minnow (*Hybognathus placitus*), and western silvery minnow (*H. argyritis*). Transactions of the Nebraska Academy of Sciences 21: 99-108.

Hurlbert, S. H. 1971. The non-concept of species diversity: a critique and alternative parameters. Ecology 52: 577-586.

Johnson, R. A., and D. W. Wichern. 1992. Applied multivariate statistical analysis. Prentice Hall, New Jersey.

Klecka, W. H. 1975. Discriminant analysis. Page 435 *in* N. H. Nie, C. H. Hall, T. G. Jenkins, K. Steinbrenner, and D. H. Brent, editors. Statistical Package for the Social Sciences, 2nd edition. McGraw-Hill, New York.

Kleinbaum, D. G., L. L. Kupper, K. E. Muller, and A. Nizam. 1998. Applied regression analysis and other multivariable methods. Brooks/Cole Publishing Company, Pacific Grove, California.

Kuehne, R. A. 1962. A classification of streams, illustrated by fish distribution in an eastern Kentucky creek. Ecology 43: 608-614.

Layher, W. G. 1994. Changes in fish community structure from a flood control dam in a Flint Hills stream, Kansas with emphasis on the Topeka shiner. American Fisheries Society Annual Meeting Abstract: 124: 147-148.

Leopold, L. B., M. G. Wolman, and J. P. Miller. 1964. Fluvial processes in geomorphology. W. H. Freeman, San Francisco, California.

Ligon, F. K., W. E. Dietrich, and W. J. Trush. 1995. Downstream ecological effects of dams. BioScience 45:183-192.

Mahalanobis, P. C. 1936. On the generalized distance in statistics. Proceedings of the National Institute of Science of India 12: 49-55.

McNeely, D. L. 1982. Niche relationships of the cyprinid fishes of spring creek, a tributary of the Neosho River, Oklahoma. Doctoral dissertation. Oklahoma State University, Stillwater.

Minckley, W. L. 1991. Native fishes of the Grand Canyon region: an obituary? Pages 124-177 *in* G. R. Marzolf, editor. Colorado River Ecology and Dam

Management. American Association for the Advancement of Science, Washington, D. C.

Ozanne, R. L. 1972. The ecology of the silvery minnow in the Platte River system of Buffalo County, Nebraska. Unpublished paper, Biology Department, Kearney State College, Kearney, Nebraska.

Penaz, M., V. Barus, and M. Prokes. 1999. Changes in the structure of fish assemblages in a river used for energy production. Regulated Rivers: Research and Management 15: 169-180.

Pflieger, W. L. 1975. The fishes of Missouri. Missouri Department of Conservation, Jefferson City.

Pflieger, W. L., and T. B. Grace. 1987. Changes in the fish fauna of the lower Missouri River, 1940-1983. Pages 166-177 *in* W. Matthews and D. Heins, editors. Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press, Norman.

Reigh, R. C. and D. S. Elsen. 1979. Status of the sturgeon chub (*Hybopsis gelida*) and sicklefin chub (*Hybopsis meeki*) in North Dakota. Prairie Naturalist 11: 49-52.

SAS. 1990. SAS System. SAS Institute Inc., Cary, North Carolina.

Schmidt, J. C., R. H. Webb, R. A. Valdez, G. R. Marzolf, and L. E. Stevens. 1998. Science and values in river restoration in the Grand Canyon. BioScience 48: 735-747.

Simberloff, D. 1972. Properties of the rarefaction diversity measurement. American Naturalist 106: 414-418.

Smith, B., and J. B. Wilson. 1996. A consumer's guide to evenness indices. Oikos 76: 70-82.

Statsoft, Inc. 1997. Statistica user's guide. 1997 edition. Statsoft Incorporated, Tulsa, Oklahoma.

Stewart, D. D. 1981. The biology of the sturgeon chub (*Hybopsis gelida* Girard) in Wyoming. Master's thesis. University of Wyoming, Laramie.

USGS (U. S. Geological Survey). 1999. Water resource and streamflow data homepage. www.waterdata.usgs.gov/nwis-w/mt.

Walker, K. F., and M. C. Thoms. 1993. Environmental effects of flow regulation on the Lower River Murray, Australia. Regulated Rivers Research and Management 8: 103-119.

Werdon, Selena J. 1992. Population status and characteristics of *Macrhybopsis gelida*, *Platygobio gracilis*, and *Rhinichthys cataractae* in the Missouri River Basin. Master's thesis. South Dakota State University, Brookings.

Werdon, S. J. 1993a. Status report on sicklefin chub (*Macrhybopsis meeki*), a candidate endangered species. Report of the U. S. Fish and Wildlife Service, Bismarck, North Dakota.

Werdon, S. J. 1993b. Status report on sturgeon chub (*Macrhybopsis gelida*), a candidate endangered species. Report of the U. S. Fish and Wildlife Service, Bismarck, North Dakota.

Williams, C. B. 1964. Patterns in the balance of nature. Academic Press, London.

Young, B. A., T. L. Welker, M. L. Wildhaber, C. R. Berry, and D. Scarnecchia, editors. 1997. Population structure and habitat use of benthic fishes along the Missouri and Lower Yellowstone River. 1997 Annual Report of Missouri River Benthic Fish Study PD-95-5832 to the U. S. Army Corps of Engineers and the U. S. Bureau of Reclamation.

CHAPTER 4

Habitat Alterations, Fish Ecomorphology, and Fish Community Structure in the Missouri River System

ABSTRACT

In 1997 and 1998, sampling was conducted on the Missouri River to determine if fish body morphology and habitat alterations can interact to influence fish community structure in altered reaches of a large river and to examine the relationship between streamlining and current velocity for a variety of fish species. The study area consisted of a moderately altered segment and two highly altered segments of the Missouri River from the mouth of the Yellowstone River to Kansas City, Missouri. One highly altered segment was impacted by a mainstem dam and the other by river channelization. The three segments exhibited greatly different fish communities. Small native minnows (Cyprinidae), particularly flathead chub (*Platygobio gracilis*), and deep-bodied suckers, such as bigmouth buffalo (*Ictiobus cyprinellus*), were common in the moderately altered segment. The highly altered below-dam segment was dominated by the dorsally compressed white (*Catostomus commersonii*) and longnose (*Catostomus catostomus*) suckers. Gizzard shad (*Dorosoma cepedianum*) dominated the fish community in the highly altered channelized segment, but were not found in the moderately altered or below dam segments. The highest mean and highest maximum current velocity use in the three segments was exhibited by species such as sicklefin chub (*Macrhybopsis meeki*), sturgeon chub (*Macrhybopsis gelida*), blue sucker (*Cycleptus elongatus*), and stonecat (*Noturus flavus*), that were optimally or nearly optimally streamlined (Fineness Ratios (FRs) $\cong 4.5$). Deep-bodied species with FRs typically below 3.5, such as buffalo fish, river carpsucker (*Carpiodes carpio*), and centrarchids, tended to exhibit the lowest mean and lowest maximum current velocity use in the three segments.

In the moderately altered segment, higher diversity of depths and current velocities led to a fish community that was less streamlined and that exhibited greater FR diversity than in the two highly altered segments, which had lower

diversities of depths and velocities. The more natural river flow characteristics and habitat conditions found in the moderately altered segment were responsible for diversities of depths, velocities, and FRs that were higher than those found in the two highly altered segments. Based on results from this study, alterations to large rivers and fish morphology can interact to change fish community structure.

INTRODUCTION

Regulation and impoundment of large rivers, including damming and channelization, have resulted in major habitat changes in these important aquatic systems. Dams, which have been referred to as a cataclysmic event in the life of a riverine ecosystem (Gup 1994), interrupt ecological processes by reducing nutrient flow, altering temperature regimes, trapping sediment, and changing the frequency and timing of discharge (Hesse 1987, Ligon et al. 1995, Poff et al. 1997). Channelization, the artificial straightening and dredging of rivers, modifies or eliminates natural river features such as channel meandering and pool-riffle sequence and changes river hydrology and morphology (Swales 1988). The loss of these features from channelization results in more uniformity in river characteristics, including depths, velocities, and substrates. The result is a more uniform habitat for riverine fishes.

The effects of dams and channelization on fish diversity, richness, density, and productivity have been well documented (Portt et al. 1986, Swales 1988, Neves and Angermeier 1990, Brittain et al. 1993, Agostinho and Zalewski 1995, Jurajda 1995, Kubečka and Vostradovský 1995). Their impacts on fish community structure have also been examined, but few studies have analyzed the links between fish community structure, stream characteristics (natural versus altered), and fish morphology.

In the evolution of stream fish, environmental conditions influence fish physiology, behavior, and morphology (Moyle and Cech 1988, Danzmann et al. 1993, Fujii 1993). An important environmental factor that fish respond to is current velocity. Prior to the turn of the century, the Missouri River hydrosystem was characterized by a diversity of habitats exhibiting a wide range of velocities (Hesse and Sheets 1993). Today, in reaches of the Missouri River that retain some

naturalness, a diversity of river habitats exists, whereas in more altered reaches, habitats tend to be more uniform. The environmental differences between these two types of reaches, especially as manifested by current velocity, must influence fish community structure.

For example, faster and more uniform current coupled with the loss of fish refugia in channelized stretches of river greatly affects fish community structure. Scarnecchia (1988) reported that fish communities in channelized reaches of a prairie stream in Iowa were dominated by more streamlined fish species than were communities found in unchannelized reaches. The unchannelized reaches had more diverse velocity conditions and offered more refugia for species not optimally streamlined. In this case, stream current, coupled with the absence of refugia, helped shape fish community structure.

Nearly one-third of the Missouri River has been channelized and another one-third has been impounded by six mainstem dams. The free-flowing Missouri River was turbid (Evermann and Cox 1896) and exhibited frequent flooding and high hydraulic diversity. Since the early twentieth century, it has been characterized by reduced sediment transport and a more stable hydrograph – a result of dam construction and land use practices throughout the basin (Hesse 1987, Hesse et al. 1989). Its once shallow and meandering channel has been channelized for navigation, primarily between Sioux City, Iowa and St. Louis, Missouri. Only one-third of the Missouri remains free-flowing and relatively unaltered.

Missouri River segments exhibit different hydrological and morphological characteristics. Some riverine segments are similar to the historic Missouri River whereas other segments are greatly altered by channelization and impoundment (Hesse et al. 1989, Hesse and Sheets 1993, Young et al. 1997). The hydrologic and morphologic diversity of Missouri River segments presents an opportunity to examine the influence of dams and channelization on fish community structure. The objectives of this study were: (1) to determine if streamlining can be a significant factor influencing fish community structure in altered reaches of a large river. (2) to examine the relationship between streamlining and current velocity for a variety of fish species in a large river.

Two main hypotheses were tested. It was hypothesized that fish communities in more altered river segments should exhibit more optimal streamlining and exhibit less variability from optimal values because of the presence

of more uniform velocities and less refugia; fish communities in less altered segments should exhibit more variation from optimal streamlining.

Second, it was hypothesized that segments that have less habitat diversity (less variability in depths, velocities, and substrates) would have a fish community characterized by less diversity in streamlining.

PHYSICAL SIGNIFICANCE AND MEASUREMENT OF STREAMLINING

It was realized long ago that certain species of fish possess body types that allow them to move more easily through the water or hold their position in high current (Gibbs-Smith 1962). There are three main forces that act on bodies that move in fluids: inertial, viscous, and gravitational. The first two are significant for bodies that are submerged and interact to produce drag. How drag is produced and how it affects submerged objects is described by Webb (1975): "The boundary layer is the region of flow around a body where the fluid velocity increases from that of the body to that of the undisturbed fluid of the stream. In the flow pattern around any solid body the velocity field becomes distorted in the region of the body. This distortion in the flow produces streamwise (i.e., in the direction of flow), favorable, and adverse pressure gradients. If there is a difference in the two gradients and the flow remains distorted downstream of the body, there is a pressure difference between leading and trailing edges which is a drag force. The magnitude of this pressure drag force depends on the magnitude of the adverse pressure gradient, for if it causes the boundary layer to separate, flow is markedly distorted downstream, and pressure drag correspondingly higher". For objects that are elongate and taper to a point, fluid gradually decelerates in the rear, little or no separation of the boundary layer occurs, and the object is pushed forward by the wedge-like closure of the fluid behind it (Vogel 1981).

A streamlined body is designed to have zero pressure drag in a fluid. In practice this is not possible and a streamline body is defined as a body with least resistance (Webb 1975). Streamlining can be described by the Fineness Ratio (FR) = l/d, where l is the total length of the body (excluding fins), also known as the standard length (measured from the tip of the fish's snout to the base of the tail fin),

and d is the maximum diameter of the body (excluding fins). A streamlined fish is one with a body shape that allows the fish to hold its position in relatively high velocity currents. The fineness ratio is a quantitative measurement that partially describes how streamlined a fish is. The fineness ratio believed to reflect an "optimal" level of streamline-ness is 4.5 and for fish this value gives minimum drag for maximum body volume (Webb 1975). FR can vary between about 3 and 7 and result in only about a 10% change in drag from the optimum value.

STUDY AREA

The relationship between fish morphology and habitat alteration was examined in three Missouri River segments. Two of the study segments are located in the state of North Dakota. One North Dakota segment extends from the Yellowstone-Missouri River confluence (Missouri River km (rkm) 2546.0) near the North Dakota-Montana border to its lower boundary of Lake Sakakawea (rkm 2470.3) and is hereafter referred to as Missouri River Benthic Fish Study segment 10 (segment 10; Figure 4.1). The second North Dakota segment extends from Garrison Dam (rkm 2235.4) in south-central North Dakota to its lower boundary of Lake Oahe (rkm 2051.9) near the North Dakota-South Dakota border and is hereafter referred to as Missouri River Benthic Fish Study segment 12 (segment 12; Figure 4.1). The third study segment is located along the Kansas-Missouri border and extends from its upper boundary at St. Joseph, Missouri (rkm 708.1) to its lower boundary near Kansas City, Missouri (rkm 591.4) and is hereafter referred to as Missouri River Benthic Fish Study segment 22 (segment 22; Figure 4.1).

The three segments exhibit differing levels of modification. Segment 10 is the least altered study segment. This segment is free-flowing with a semi-natural hydrograph, a result of the merging of the free-flowing Yellowstone River and the Missouri River, which is regulated upriver by Fort Peck Dam. This segment is characterized by high main channel turbidity, no major shoreline development, and few revetment banks (rip-rap). The lack of shoreline development and revetment banks allows the main river channel to meander naturally, which creates a diversity of off-channel habitats. Segment 12, in contrast, exhibits fewer pre-impoundment physical and biological characteristics. Garrison Dam and Lake Sakakawea have

created an alluvium sink, thereby reducing the sediment load in the river below the dam (Berkas 1995). The river below the dam is uncharacteristically clear and natural aggradative and degradative processes have been disrupted. The dam strongly regulates the hydrograph. Furthermore, hypolimnetic withdrawals from Lake Sakakawea have created uncharacteristically cool water temperatures during the summer with maximum summer temperatures approximately 9 °C cooler than before impoundment (Everett 1999). This segment is also characterized by numerous revetments and a high degree (25-40%) of shoreline development and bank stabilization.

Segment 22 is the most heavily modified of the three study segments. Wing-dams, dikes, and rip-rap have been used to form and maintain a navigation channel. These modifications have significantly narrowed and deepened the river channel (Sayre and Kennedy 1978), changing the depth-velocity profile and reducing the diversity of depths, velocities, and substrates in the river (Hesse and Sheets 1993). These structures also prevent natural meandering of the main river channel.

METHODS

Data Collection

Fish community and habitat data for this study were obtained from Missouri River Benthic Fish Study data collected in 1997 and 1998. A stratified random sample was used to collect fish in the three study segments where the strata were macrohabitat types. These macrohabitats were main channel cross-over, outside bend, inside bend, secondary channel: non-connected, secondary channel: connected, tributary mouth (Figure 4.2). In the segments, macrohabitats served as sampling units. In each segment, fish were collected from five randomly selected sample units of each stratum from July through September in both 1997 and 1998. A variety of fish capturing gears were used that sampled a wide variety of species and sizes, thereby ensuring accurate description of the fish community in each segment. These gears were a bag seine (10.7 m long, 1.8 m high, 1.8 m^3 bag, 5 mm mesh), a benthic beam trawl (2 m wide, 0.5 m high, 5.5 m long, 3.2 mm inner bag mesh), a trammel net (22.9 m long, inner wall 2.4 m deep with 2.5 cm mesh, outer wall 1.8 m deep with 20.3 cm mesh), an electrofishing boat (Coffelt VVP-15

variable voltage pulsator, 5,000 W generator), a gill net (30.5 m long, 1.8 m high, mesh sizes of 1.9 cm, 3.8 cm, 5.1 cm, 7.6 cm), and a hoop net (4.8 m in length, 3.7 cm diameter mesh, finger style throat, seven fiberglass hoops, and a 15.2 m lead attached to the first hoop made of 3.8 cm mesh). Gear selectivity and efficiency bias among the gear types could have existed but were not evaluated empirically. A subsample was a single gear sample.

Water depth (m), velocity (m/sec), and substrate (% silt, % sand, % gravel) were measured at each subsample following the successful deployment and retrieval of fish collection gears and later used to characterize segments and segment macrohabitats (for an in-depth description of habitats, measurement of habitat physiochemical variables, and fish collection techniques, see Sappington et al. 1998). In macrohabitat sample units greater than 1.5 m in depth, a boat was anchored at the proper location and current velocity was measured with the aid of an A55M sounding reel and hangar bar (19.1 mm x 304.8 mm). A Marsh-McBirney Flowmate Model 2000 probe was attached to the hangar bar and lowered near bottom with the sounding reel. A 22.7 kilogram sounding weight was used to keep the current velocity meter probe pointed into the current and positioned directly below the boat. Current velocity was measured to the nearest 0.1 m/sec. Water depth was measured with a Lowrance sonar device to the nearest 0.1 m.

A bottom substrate sample was collected with an iron pipe that had one end closed. One end of a nylon rope was attached to the open end of the pipe and the other connected to the boat. The pipe was then dragged through the area of the gear sample. The pipe contents were emptied onto the boat and the percentage of silt (particle size <= 0.06 mm), sand (particle size 0.06 <= 2.0 mm), and gravel (particle size 2.0 mm <= 16 mm) were visually estimated. Later, the geometric mean of substrate size was calculated for each subsample (McMahon et al. 1997).

Depth, velocity, and substrate were also measured with the same devices in shallow macrohabitat replicates at each fish collection subsample. Water column depth and water velocity were measured with the aid of a standard wading rod at three points along the gear sampling area. A substrate sample was collected with the iron pipe by dragging it along the area sampled by the fish collecting gear. Percentages of sand, silt, and gravel were then estimated from the pipe contents.

Fish Communities

Fineness Ratio

In 1998, the standard body length and maximum body depth of 10-20 fish for each species was measured for calculating FRs in segments 10 and 12. For segment 22, standard body length and maximum body depth were measured for most species from museum specimens collected from this segment in 1992 and later housed at Sternberg Museum of Natural History (Fort Hays State University, Hays, Kansas). For species in this segment for which there were no museum specimens, FRs were obtained from other Missouri River segments or from the literature (Tomelleri and Eberle 1990, Cross and Collins 1995). Bow calipers (300 mm gape) were used to measure maximum body depth for large fish, whereas dial calipers (150 mm gape) were used to measure maximum body depth for small fish. Standard body length and maximum body depth were recorded to the nearest 0.01 mm. For some species of fish, changes in morphology associated with ontogeny can occur (Reis et al. 1998, Hood and Heins 2000). Therefore, plots of FR versus standard length were constructed for most individual species to determine if FR remained constant over a variety of fish lengths. If FR changed as fish length increased, fish were separated into two length groups and FR computed for each of these groups.

Mean community FR for each segment was calculated by weighting according to relative abundances of the different species, i.e., by dividing the number of individuals of a species by the total number of individuals for all species. Relative abundances were calculated for all species for which FRs were obtained. No species in any segment with a relative abundance greater than 0.1% were excluded from analysis. Weighted FR means were then calculated for each river segment by multiplying the relative abundance of each species by its mean ratio, and summing for all species in the segment. Additionally, a combined weighted mean FR was also computed for the three main channel macrohabitats (main channel cross-over, inside bend, outside bend) in each study segment. Fish in these three habitats were assumed to be most influenced by anthropogenic disturbance and current velocity. Deviation of segment weighted mean FRs from optimal (4.50) was determined by subtracting each weighted FR value from 4.50.

FRs were also computed for each macrohabitat in a segment to examine the relationship between FR and macrohabitat physical conditions. First, the FRs for

each macrohabitat subsample were weighted by fish relative abundance and summed, obtaining a weighted FR for the subsample. Then, the subsample FRs were averaged to obtain the replicate FR. Next, replicate FRs were averaged to obtain the macrohabitat mean FR for a year. Finally, yearly FR means were averaged for each macrohabitat type.

Variability in FR was examined using coefficient of variation (CV), the standard deviation divided by the mean (Zar 1984). For each segment, CV was calculated for each macrohabitat replicate in a year. Then, macrohabitat replicate values were averaged, giving the yearly mean for each macrohabitat type. Finally, yearly macrohabitat CV values were averaged.

Variation in FR across macrohabitat types was also computed for each segment. CV values obtained for each macrohabitat type were averaged within years. Finally, yearly values were averaged, yielding the CV for the segment.

Fish Composition and Heterogeneity

Community attributes are key to explaining and describing the relationship among fish community structure, stream characteristics, and fish morphology. Therefore, fish family and species composition, species diversity, and species evenness were determined for each river segment.

Fish community diversity was examined in each segment by computing measures of species heterogeneity, richness, and evenness. Species heterogeneity in each segment was determined with the reciprocal of Simpson's index (Williams 1964).

(4.1) $D = \sum p_i^2$ (i=1,.....,s fish species)

where D is Simpson's index, p_i is the proportion of fish species i in the community, and $\sum p_i = 1.0$.

Fish species diversity was quantified with the equation:

(4.2) $1/D$ = fish species diversity

where 1/D is the reciprocal of equation *(4.1)* which varies from 1 to s, the number of species in the sample.

Species richness was examined with the rarefaction method (Hurlbert 1971, Simberloff 1972). This method was chosen over other richness measures because

it corrects for differences in sample size. Species evenness for each segment was computed with Smith and Wilson's index (Smith and Wilson 1996).

(4.3) $E = 1 - \left[2/\left(\pi \arctangent\left\{\sum_{i=1}\left(\log_e(n_i) - \sum_{j=1}(\log_e(n_j)/s\right)^2/s\right\}\right)\right]$

where E is Smith and Wilson's index of evenness, n_i is the number of individuals in species i in sample (i=1, 2, 3, 4,......,s), n_j is the number of individuals in species j in sample (j=1, 2, 3, 4,......,s), and s is the number of species in the entire sample.

According to Smith and Wilson (1996), this is the best available index of evenness because it is independent of species richness and is sensitive to both rare and common species in the community.

Additionally, the diversity and evenness of fish among various FR categories were examined for each segment. FR categories were classified as <3.00, 3.00-3.49, 3.50-3.99, 4.00-4.49, 4.50-4.99, 5.00-5.49, 5.50-5.99, and >5.99.

Physical Characteristics and Fish

For this study, the physical conditions in each segment were characterized at the macrohabitat level. Mean velocity, depth, and substrate size were computed by first averaging subsample measurements taken at a macrohabitat replicate. Next, replicates were averaged, giving the yearly mean for each macrohabitat type. Finally, yearly values were averaged to obtain the overall mean depth, velocity, and substrate size for each macrohabitat type.

Variation in depth, velocity, and substrate within and across macrohabitat types in each segment was determined with CV. Calculation of CV for the three physiochemical variables followed the procedures used for computing CV for FR.

Mean current velocity use and maximum current velocity use by fish were examined for each species and for various FR categories (FR categories = <3.00, 3.00-3.49, 3.50-3.99, 4.00-4.49, 4.50-4.99, 5.00-5.49, 5.50-5.99, >5.99). Mean use for individual species was computed using subsample observations. A subsample taken within a macrohabitat replicate that contained at least one fish was considered an observation for a species. These observations were averaged to obtain the mean current velocity used by the species. Mean use for each FR category was obtained by first computing the mean current velocity used by each species. Then, species were placed into categories based on their FR. Finally, mean velocity values for species in a category were averaged. The maximum current velocity

used by a species or a FR category is the highest current velocity measured in a subsample observation containing a species or a species from a FR category. Use by FR categories was examined for each segment using bar plots.

Statistical Analyses

Each of the six macrohabitat types was found in each segment; however, not all types were common enough among segments to permit statistical comparison of their physiochemical variables and fineness ratios. Therefore, mean fineness ratio, current velocity, depth, and substrate were compared among segments for only main channel cross-over, outside bend, and inside bend in each segment by performing Friedman's analysis of variance on ranks (Friedman 1937) with segments serving as treatments and years as blocks. The test statistic, Friedman's X_r^2, is calculated as:

$$(4.4) \quad X_r^2 = 12 \, / \, (ba(a+1)) * \Sigma_{i=1} R_i^2 \text{-} 3b(a+1)$$

where b = years (blocks), a = segments (treatments), and R_i = summed ranks for each segment (i=1,..,3).

A Tukey-type multiple comparison procedure for ranked data was performed following a significant ANOVA (Zar 1984). Differences in FR, current velocity, depth, and substrate variation among segments for main channel cross-over, outside bend, and inside bend macrohabitats were also examined with Friedman's analysis of variance on ranks (Friedman 1937).

Relations between habitat variables and fish communities were evaluated with regression methods. Linear least-squares regression was used to examine the relationship between FR variability and variability in physiochemical variables among macrohabitat types. FR variability (expressed as CV) served as the dependent variable (Y) and variability (expressed as CV) in current velocity, depth, and substrate size served as predictor variables (X_j). For each physiochemical variable, this analysis was used to test the $H_o = \beta_1 = 0$, i.e., there is no linear relationship between FR variability and variability in the physiochemical variable (current velocity, depth, or substrate size). Multiple linear regression was also used to describe the relationship between variability in current velocity, depth, and substrate size and FR variability.

$$(4.5) \quad Y = \beta_0 + \Sigma_{j=1} \beta_j X_j \quad \text{(j=1,........,n environmental variables)}$$

where Y is FR variability, β_0 is the y-intercept, β_j is the slope for each environmental variable, and X_j represents the environmental variables. This analysis was used to test the $H_o = \beta_1 = \beta_2 = \beta_3 = 0$, i.e., there is no linear relationship between FR variability and variability in the physiochemical variables (current velocity, depth, or substrate size). For multiple regression modeling, predictor variable collinearity was examined with a correlation matrix and multicollinearity was examined by computing variance inflation factor (Hair et al. 1995). Influential observations for best fitted models were identified with Cook's distance. Heteroscedasticity was examined with residual plots and normality of the error term distribution was examined with normal probability plots.

RESULTS

Composition and Heterogeneity of Fish Communities

Species and family composition differed greatly among the three segments. Small native minnows (Cyprinidae), particularly flathead chub (*Platygobio gracilis*; Table 4.1) were common in segment 10, constituting 55% of the fish there (Table 4.2), whereas in segments 12 and 22, minnows constituted only 3% and 27% of the fish, respectively (Table 4.2). Goldeye *(Hiodon alosoides*; 16%) and native deep-bodied suckers such as bigmouth buffalo (*Ictiobus cyprinellus*) and smallmouth buffalo (*Ictiobus bubulus*) (Catostomidae; 17%) were also common in segment 10. Flathead chub was also the most common fish caught in the three main channel habitats (main channel cross-over, inside bend, outside bend) of segment 10, constituting 37% of the catch there (Table 4.1).

Segment 12 was dominated by dorsally compressed suckers (Catostomidae) which constituted 94% of the fish (Table 4.2). Most of these fish (91% of total fish) were white (*Catostomus commersonii*) and longnose (*Catostomus catostomus*) suckers less than150 mm in total length (Table 4.3). In the three main channel habitats shovelnose sturgeon (*Scaphirhynchus platorynchus*) and fathead minnow (*Pimephales promelas*) made up over 55% of the catch. Many native species of Cyprinidae and deep bodied Catostomidae found in segment 10 were absent in segment 12.

Gizzard shad (*Dorosoma cepedianum*) were common in channelized segment 22, constituting 43% of the fish there (Table 4.4). This species was absent from both segments 10 and 12 . In addition, catfishes (Ictaluridae) were common in segment 22, constituting 11% of the fish (Table 4.2). In the three main channel habitats, gizzard shad and emerald shiner (*Notropis atherinoides*) constituted over 50% of the catch.

Species diversity, richness, and evenness differed greatly among the segments. Species heterogeneity was highest in least altered segment 10 (1/D=6.88, equation *4.2*) and lowest in segment 12 (1/D=1.67) (Table 4.5). Species richness was similar in segments 10 (28.46) and 22 (31.72) and higher than that found for segment 12 (15.72) (Table 4.5). Evenness was highest in segment 10 (E=0.23, equation *4.3*) and lower and similar in segments 12 (E=0.17) and 22 (E=0.16) (Table 4.5).

Physical Characteristics of Segments and Habitats

Overall, segment 10 exhibited highest variability in habitat features of the three segments. Variation in velocity (coefficient of variation = 1.40) and in depth (1.14) when computed across all macrohabitat types was highest in segment 10. Variation in depth across macrohabitats was lowest in segment 12 (0.95; segment 22=0.96), whereas velocity variability was lowest in segment 22 (1.15; segment 12=1.21). Segments 10 (2.46) and 12 (3.13) exhibited the highest substrate variation. Segment 22 had the lowest variation in substrate (1.24).

Among the three segments, main channel cross-over tended to exhibit greater depths and velocities than other macrohabitats (Tables 4.6-4.8). The coarsest substrate was found in outside bend macrohabitat in the three segments, with segments 22 and 12 exhibiting much coarser substrate in this habitat than segment 10. Segment 10 tended to have the least coarse substrate when compared with segments 12 and 22 across macrohabitat types (Tables 4.6-4.8).

Variability in depth, current velocity, and substrate differed among macrohabitats and segments. Secondary channel: connected exhibited the highest depth and current velocity variability of all macrohabitats in segments 10 (coefficient of variation = 1.27) and 12 (1.00), whereas in segment 22 the highest depth and current velocity variability was exhibited by outside bend (1.12) and tributary mouth (3.07) macrohabitats (Tables 4.6-4.8), respectively. Main channel cross-over

macrohabitat tended to exhibit little variability in depth and current velocity in the study segments.

The macrohabitats that exhibited the highest substrate variability differed among segments. Outside bend (coefficient of variation = 0.86), main channel cross-over (1.75), and tributary mouth (2.03) macrohabitats exhibited the highest substrate variability in segments 10, 12, and 22, respectively (Tables 4.6-4.8). Secondary channel: non-connected exhibited low substrate variability in all study segments.

For most macrohabitats, mean depth, mean current velocity, and mean substrate size differed significantly among segments (ANOVA, $P<0.05$; Table 4.9). Macrohabitat depth, current velocity, and substrate size tended to differ significantly between segment 22 and segments 10 and 12 ($P<0.05$), whereas segments 10 and 12 did not tend to differ significantly from one another ($P>0.05$) (Table 4.9). However, inside bend current velocity ($P=0.21$) and main channel cross-over substrate ($P=0.72$) did not differ significantly among segments. Variation in mean macrohabitat depth, current velocity, and substrate was not significantly different among the three river segments (Table 4.10).

Streamlining and Fineness Ratio

Fish communities in highly altered segments 12 and 22 exhibited weighted mean FRs that were closest to optimal. Segment 12 exhibited the mean FR with the smallest deviation from optimal computed from all six macrohabitat types (0.37), but had the FR with the largest deviation from optimal from the three main channel habitats (1.06). The mean FR computed from the three main channel habitats with the smallest deviation from optimal was found for segment 22 (0.12) however, this segment exhibited the FR with the largest deviation from optimal from all six macrohabitat types (0.81). For segment 10, the mean FR computed from all six macrohabitat types and from the three main channel habitats deviated 0.42 and 0.23 from optimal, respectively.

The three segments exhibited different weighted mean FRs. Segment 12 exhibited the highest mean FR computed from all six macrohabitat types (4.87) as well as the highest FR from the three main channel habitat types (5.56; main channel cross-over, inside bend, outside bend). For segment 10, the mean FR computed from all macrohabitat types was less than optimal (4.08), but was greater

than optimal (4.73) from the three main channel macrohabitats. Segment 22 exhibited the lowest mean FR (3.69), but had the FR closest to optimal (4.38) from the three main channel habitats. Variation in weighted mean FRs when computed across macrohabitat types was highest in segment 10 (0.33), second highest in segment 22 (0.26), and lowest in segment 12 (0.25).

Weighted mean FRs in macrohabitats were highest in segment 12 and lowest in segment 22 when identical macrohabitat types were compared across segments (Tables 4.6-4.8). Variation in macrohabitat mean FRs followed this trend as well (Tables 4.6-4.8). Variation in mean FRs in main channel cross-over, inside bend, and outside bend macrohabitats did not differ significantly, however, among the segments (Table 4.10) and mean FRs differed significantly only between segments 10 and 22 (Table 4.9).

Variation in FRs tended to be lowest in macrohabitats with uniform velocities and substrates. Among macrohabitat types, variation in FRs was positively related to variation in velocities in the three segments (segment 10, $r=0.59$, $P=0.04$; segment 12, $r=0.59$, $P=0.04$; segment 22, $r=0.81$, $P=0.0044$). This relation existed for substrate size in the three segments as well (segment 10, $r=0.61$, $P=0.04$; segment 12, $r=0.65$, $P=0.02$; segment 22, $r=0.85$, $P=0.0020$) (Table 4.11). Variation in FRs was not related to depth variation in any of the segments ($P>0.10$; Table 4.11). CV of substrates in a multiple regression equation explained 61% of the variation in FRs ($P=0.0084$).

Streamlined fishes such as sicklefin chub (*Macrhybopsis meeki*), sturgeon chub (*Macrhybopsis gelida*), and stonecat (*Noturus flavus*) that use sand-gravel habitat with steady velocities were common in segment 10, but were absent in segment 12 and rare in segment 22 (Tables 4.1-4.3). These species, and other streamlined fishes, were most commonly found in main channel macrohabitats that exhibited the highest current velocities (main channel cross-over, inside bend, outside bend) however, few fish of any species were captured in main channel cross-over habitat in segments 12 and 22 (Tables 4.1-4.3). Deep-bodied, poorly streamlined fishes, such as common carp (*Cyprinus carpio*), gizzard shad, and buffalo fish (*Ictiobus* spp.) were common in segments 10 and 22, but not in segment 12 (Tables 4.1-4.3). These types of fish were virtually absent from main channel cross-over habitat, which exhibited the highest current velocities, and were almost always found in macrohabitats with low current velocities (secondary channel: non-

connected, tributary mouth) in all segments. In segment 12, relative abundance was low in all macrohabitats for fish exhibiting FRs less than 4.5.

The distribution of fish among FR categories was more uniform in segment 10 (E=0.70, equation 4.3) than in segments 12 (E=0.18) and 22 (E=0.16) (Figure 4.3). FR category heterogeneity was highest for segment 10 (1/D=5.65, equation 4.2) and lowest for segment 12 (1/D=1.12; segment 22, 1/D=2.56). When only main channel cross-over, inside bend, and outside bend macrohabitats were considered, segment 10 exhibited the highest evenness (E=0.65) (Figure 4.4) and diversity (1/D=4.37). The lowest diversity was found for segment 22 (1/D=2.90; segment 12, 1/D=2.95), whereas the lowest evenness was found for segment 12 (E=0.07; segment 22, E=0.18).

The highest mean and highest maximum current velocity use in the three segments was exhibited by species such as sicklefin chub, sturgeon chub, blue sucker (Cycleptus elongatus), and stonecat, that were optimally or nearly optimally streamlined (FRs≅4.5; Tables 4.12-4.14). However, shovelnose sturgeon also was frequently found in habitats with high current velocities even though it possessed a non-optimal FR (≅8.5). Deep-bodied species with FRs typically below 3.5, such as buffalo fish, river carpsucker (Carpiodes carpio), and centrarchids, tended to exhibit the lowest mean and lowest maximum current velocity use in the three segments (Tables 4.12-4.14). Examples of different body forms exhibited by fish captured in this study are depicted in Figure 4.5.

In the Missouri River, body shape may impose a physical limit on the types of habitats in which a fish can live. Mean current velocity use among FR categories tended to be highest for fish such as sicklefin chub and sturgeon chub with FRs greater than 4.5, whereas the lowest mean current velocity use was exhibited by fish such as river carpsucker and common carp with FRs less than 4.0 (Figure 4.6). The maximum current velocity used by any species in a segment was highest for fish with near optimum FRs (Figure 4.7), and tended to be lowest for fish that exhibited FRs below 4.0. However, the lowest maximum current velocities used in segment 22 were found for fish exhibiting FRs between 3.5-4.0 and 5.0-5.5. Fish in segments 10 and 22 with FRs greater than 4.5 tended to use a greater diversity of current velocities than less streamlined fish (Figures 4.8 and 4.10) whereas most fish in segment 12 generally used similar, low current velocities (Figure 4.9).

DISCUSSION

Community Fineness Ratio

When FR and physical conditions were analyzed across all habitat types, the more natural segment 10 was characterized by higher diversities of FR, velocity, and depth than the more altered segments 12 and 22. The observed differences in diversities of depths, velocities, and FRs among segments are associated with distinct differences in flow characteristics and habitat conditions. Segment 10 is heavily influenced by the free-flowing Yellowstone River. The Yellowstone River is characterized by a high sediment load and a natural hydrograph marked by two flood pulses–one in March and one in June (Hesse et al. 1989). These natural river characteristics, coupled with minimal shoreline development and revetment structures (rip-rap), work to create a diversity of habitats and physical conditions in segment 10. Conditions in segment 10 thus selected for a diversity of fishes, some optimally streamlined, and some not (1/D=5.65, E=0.70). Conversely, modified river conditions in segments 12 and 22, resulting from main channel impoundment, channelization, and revetment structures, have reduced diversities of habitat and physiochemical characteristics (Hesse and Sheets 1993). These habitat changes have resulted in river segments with fish communities characterized by a reduced diversity of body forms.

Within most macrohabitat types however, segment 22, the most highly altered segment, was characterized by greater diversities of depths, velocities, and FRs than altered segment 12 and less-altered segment 10 (Tables 4.6-4.8). Scarnecchia (1988) examined the relationship between physical variables and FR in channelized and unchannelized reaches of a small prairie stream in Iowa. In his study, fish were sampled within study sections and section physical conditions were assessed with a transect method where conditions were measured at regular intervals perpendicular to the flow, across habitat types. This method of describing the physical conditions encountered by fish is difficult or impossible to employ in a river as large as the Missouri. An approach such as the one used in this study, where fish were sampled in habitats and the physical conditions of habitats were characterized, is the method typically employed in large rivers. Even though macrohabitats were not sampled in proportion to their availability in each river segment, examining the diversity of physiochemical variables across habitat types,

rather than conditions within habitat types, better indicates the diversity of conditions that work to influence community FR and structure. Analysis across habitat types is more appropriate because fish often move between different habitats as part of their life history (Karr et al. 1982).

Among the three segments, segment 22 exhibited the community FR closest to optimal (4.38) when the three main channel habitats were considered; when community FR was calculated using all six habitat types, however, it exhibited the FR furthest from optimal (3.69). This segment was dominated by the poorly streamlined gizzard shad. In 1998, several subsamples contained over 500 shad, heavily weighting the community FR. This species can form large schools (Cross and Collins 1995), which, if captured in schools, would increase its susceptibility to oversampling. If these subsamples were removed (totaling approximately 2,500 fish), the community FR for segment 22 increased from 3.69 to the near optimal value of 4.40.

The difference in community FRs and, in part, the differences in diversity of velocities and depths among segments, resulted from the abundance of shallow, low current velocity habitats. Segment 10 exhibited a sub-optimal community FR (4.08), whereas segment 12 exhibited a community FR above optimal (4.87) and segment 22 exhibited a near optimal community FR (4.40) if large gizzard shad subsamples were removed. Low-velocity habitats, such as secondary channel: connected and secondary channel: non-connected, that typically support large numbers of sub-optimally streamlined species (FR<4.5) were much more abundant in segment 10 than in segment 22. An abundance of these species would tend to lower the community FR. Even though these habitats were present in segment 12, the lack of sediment in this segment, resulting from sediment trapping by Garrison Dam and Lake Sakakawea (Berkas 1995), probably increased the vulnerability of many fish species to predation in these habitats and others (Everett 1999).

Streamlining and Body Form

Species which used the highest average and the highest maximum current velocities, and which would thus be expected to be near-optimally streamlined, nevertheless exhibited greatly different FRs. A few species common to higher velocities, such as longnose sucker, channel catfish (*Ictalurus punctatus*), and blue sucker were optimally streamlined (FR ≅ 4.5). Others, such as sicklefin chub, sturgeon chub, and stonecat, were nearly optimally streamlined with FRs slightly

greater than 4.5. In contrast, the shovelnose sturgeon, which used moderate to high current velocities in the three segments, was not optimally streamlined (FRs > 8.5). The explanation for these greatly different morphological types inhabiting high velocity water is suggested in an unrelated laboratory study by Webb (1989). In that study of the ability of three benthic fish species to hold their position in the current, two species, thornback ray (*Raja clavata*) and plaice (*Pleuronectes platessa*), had FRs of approximately 10, while a third species, father lasher (*Myoxocephalus scorpius*), exhibited a near optimal FR of 4.2. Webb (1989) reported that two common patterns of benthic fish body form allow fish to be proficient at station holding in current. The first form is flattened, such as plaice in Webb's (1989) study or shovelnose sturgeon in this study, which has high frontal lift, but counters high lift with low frontal drag. The second form is more fusiform, such as lasher in Webb's (1989) study or sicklefin chub in this study, which has high frontal drag, but counters high drag with low frontal lift.

Even though the fish studied by Webb (1989) relied heavily upon body characteristics to hold their position, they also used a variety of behaviors such as fin-beating and substratum grasping. Lasher, which performed poorer than plaice over smooth substratum, performed better than plaice over rough substratum. Lasher used their pectoral fins to grip the substratum surface, aiding in station holding. Perhaps species such as the sicklefin chub, which possesses elongate pectoral fins (Cross and Collins 1995) and are found in high current velocity habitats (Everett 1999), use this same behavior to aid in holding station. Webb (1989) further hypothesized that the capacity of a fish to hold station with a body form that is dorso-ventrally flattened is best over a flat, smooth substratum where it can minimize frontal lift. Adams et al. (1997) observed that shovelnose sturgeon in an experimental swim tunnel with a smooth substratum held station through substrate appression at current velocities exceeding 0.4 m/sec. Such behavior would explain why shovelnose sturgeon have been found in several studies to occupy habitats with current-swept sandy bottoms (Hurley et al. 1987, Curtis et al. 1997, Quist et al. 1999).

Two distinctly different body forms, one fusiform in shape and another dorso-ventrally flattened, were exhibited by fish using high current velocities in this study. Webb's (1989) study was an in-depth look into how current and fish morphology interact to influence station holding ability and was conducted in a controlled

environment. Such a laboratory study on Missouri River fishes might clarify the mechanisms by which native species cope with changing habitats in the altered Missouri River.

Significance

Many attempts have been made to use aspects of fish morphology to explain fish community structure (Hora 1922, Hubbs 1941, Gatz 1979, Mahon 1984, Pouilly 1993). However, only Scarnecchia (1988) has evaluated the relationship between fish morphology and habitat alteration in shaping fish community structure. His research, however, was conducted on a small stream, not a large river. Until this study, the relationship between stream alteration and streamlining and how they influence fish community structure in a large river had not been evaluated.

Damming and channelization of water courses acts to homogenize physical conditions. The effects these changes have on fish communities can be numerous and far-reaching, impacting fish growth (Orlova 1987, Beamesderfer et al. 1995), species composition (Martinez et al. 1994, Weaver and Garman 1994, Wilde and Ostrand 1999), and community structure (Bain et al. 1988, Kubečka and Vostradovský 1995, Penaz et al. 1999). In the past, research addressing the impacts that damming and channelization have had on fish community structure has focused on changes resulting from altered river physical conditions (Schlosser 1985, Bain et al. 1988, Poff and Allan 1995, Reyes-Gavilán et al. 1996). However, these studies failed to recognize that fish morphology may also play an important role in shaping fish community structure in altered reaches. Based on results from this study, alterations to large rivers and fish morphology can interact to change fish community structure.

LITERATURE CITED

Adams, S. R., G. R. Parsons, J. J. Hoover, and K. J. Killgore. 1997. Observations of swimming ability in shovelnose sturgeon (*Scaphirhynchus platorynchus*). Journal of Freshwater Ecology 12: 631-633.

Agostinho, A. A., and M. Zalewski. 1995. The dependence of fish community structure and dynamics on floodplain and riparian ecotone zone in Parana River, Brazil. Hydrobiologia 303:141-148.

Bain, M. B., J. T., Finn, and H. E. Booke. 1988. Streamflow regulation and fish community structure. Ecology 69:382-392.

Beamesderfer, R. C. P., T. A. Rien, and A. A. Nigro. 1995. Differences in the dynamics and potential production of impounded and unimpounded white sturgeon populations in the lower Columbia River. Transactions of the American Fisheries Society 124: 857-872.

Berkas, W. R. 1995. Transport and sources of sediment in the Missouri River between Garrison Dam and the headwaters of Lake Oahe, North Dakota, May 1988 through April 1991. Water-resources investigations report 95-4087. U. S. Department of the Interior, U. S. Geological Survey, Bismarck, North Dakota.

Brittain, J. E., J. A. Eie, Å. Brabrand, S. J. Saltveit, and J. Heggenes. 1993. Improvement of fish habitat in a Norwegian river channelization scheme. Regulated Rivers: Research and Management 8: 189-194.

Cross, F. B, and J. T. Collins. 1995. Fishes in Kansas. Museum of Natural History, Public Education Series, No. 14, University of Kansas, Lawrence.

Curtis, G. L., J. S. Ramsey, and D. L. Scarnecchia. 1997. Habitat use and movements of shovelnose sturgeon in Pool 13 of the Mississippi River during extreme low flow conditions. Environmental Biology of Fishes 50: 175-182.

Danzmann, R. G., M. M. Ferguson, and D. L. G. Noakes. 1993. The genetic basis of fish behaviour. Pages 3-30 in T. J. Pitcher, editor. Behaviour of teleost fishes. Chapman-Hall, London.

Everett, S. R. 1999. Ecology and life history of three native benthic fishes in the Missouri and Yellowstone River. Masters thesis. University of Idaho, Moscow.

Evermann, B. W., and U. O. Cox. 1896. A report upon the fishes of the Missouri River basin. Pages 325-429 in Part 20 for Year Ending June 30, 1894. U. S. Commission of Fish and Fisheries. U. S. of America Printing Office, Washington, D. C.

Friedman, M. 1937. The use of ranks to avoid the assumption of normality implicit in the analysis of variance. Journal of the American Statistical Association 32: 675-701.

Fujii, R. 1993. Coloration and chromatophores. Pages 535-562 *in* D. H. Evans, editor. The physiology of fishes. CRC Press, Inc., Boca Raton, Florida.

Gatz, A. J. 1979. Community organization in fishes as indicated by morphological features. Ecology 60: 711-718.

Gibbs-Smith, C. H. 1962. Sir George Cayley's aeronautics 1796-1855. H. M. Stationery, Office of the Science Museum of London.

Gup, T. 1994. Dammed from here to eternity: dams and biological integrity. Trout 35:14-20.

Hair, J. F., Jr., R. E. Anderson, R. L. Tatham, and W. C. Black. 1995. Prentice Hall, Inc., Englewood Cliffs, New Jersey.

Hesse, L. W. 1987. Taming the wild Missouri River: what has it cost? Fisheries 12(2): 2-9.

Hesse, L. W., J. C. Schmulbach, J. M. Carr, K. D. Keenlyne, D. G. Unkenholz, J. W. Robinson, and G. E. Mestl. 1989. Missouri River fishery resources in relation to past, present, and future stresses. Pages 352-371 *in* D. P. Dodge, editor. Proceedings of the International Large River Symposium. Canadian Special Publications of Fisheries and Aquatic Science, 106, Ottawa, Ontario, Canada.

Hesse, L. W., and W. Sheets. 1993. The Missouri River hydrosystem. Fisheries 18(5): 5-14.

Hood, C. S., and D. C. Heins. 2000. Ontogeny and allometry of body shape in the blacktail shiner, *Cyprinella venusta*. Copeia 2000: 270-275.

Hora, S. L. 1922. Structural and modifications in the fish of mountain torrents. Records of the Indian Museum (Calcutta) 24: 31-61.

Hubbs, C. L. 1941. The relation of hydrological conditions to speciation in fishes. Pages 182-195 *in* A Symposium on Hydrobiology. University of Wisconsin, Madison.

Hurlbert, S. H. 1971. The non-concept of species diversity: a critique and alternative parameters. Ecology 52: 577-586.

Hurley, S. T., W. A. Hubert, and J. G. Nickum. 1987. Habitats and movements of shovelnose sturgeons in the upper Mississippi River. Transactions of the American Fisheries Society 116: 655-662.

Jurajda, P. 1995. Effect of channelization and regulation on fish recruitment in a flood plain river. Regulated Rivers: Research and Management 10: 207-215.

Karr, J. R., L. A. Toth, and G. D. Garman. 1982. Habitat preservation for midwest stream fishes: principles and guidelines. Corvallis, Oregon: U. S. Environmental Protection Agency 600/3-83-006: 1-120.

Kubečka, J., and J. Vostradovský. 1995. Effects of dams, regulation and pollution on fish stocks in the Vltava River in Prague. Regulated Rivers: Research and Management 10:93-98.

Ligon, F. K., W. E. Dietrich, and W. J. Trush. 1995. Downstream ecological effects of dams: A geomorphic perspective. Bioscience 45: 183-192.

Mahon, R. 1984. Divergent structure in fish taxocenes of north temperate streams. Canadian Journal of Fishers and Aquatic Sciences 41: 330-350.

Martinez, P. J., T. E. Chart, M. A. Trammell, J. G. Wullschleger, and E. P. Bergersen. Fish species composition before and after construction of a main stem reservoir on the White River, Colorado. Environmental Biology of Fishes 40: 227-239.

McMahon, T. E., A. V. Zale, and D. J. Orth. 1997. Aquatic habitat evaluation. Pages 83-120 in B. R. Murphy and D. W. Willis, editors. Fisheries Techniques, Second Edition. American Fisheries Society, Bethesda, Maryland.

Moyle, P. B., and J. J. Cech, Jr. 1988. Fishes: an introduction to ichthyology. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.

Neves, R. J., and P. L. Angermeier. 1990. Habitat alteration and its effects on native fishes in the upper Tennessee River system, east-central U.S.A. Journal of Fish Biology 37 (supplement A): 45-52.

Orlova, E. L. 1988. Peculiarities of growth and maturation of the catfish, Silurus glanis, in the Volga Delta under regulated flow conditions. Journal of Ichthyology 28: 35-45.

Penaz, M., V. Barus, and M. Prokes. 1999. Changes in the structure of fish assemblages in a river used for energy production. Regulated Rivers Research and Management 15: 169-180.

Poff, N. L., and J. D. Allan. 1995. Functional organization of stream fish assemblages in relation to hydrological variability. Ecology 76: 606-627.

Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegaard. B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime: A paradigm for river conservation and restoration. Bioscience 47: 769-784.

Portt, C. B., E. K. Balon, and D. L. G. Noakes. 1986. Biomass and production of fishes in natural and channelized streams. Canadian Journal of Fisheries and Aquatic Sciences 43: 1926-1934.

Pouilly, M. 1993. Habitat, ecomorphology, and fish community structure in three tropical streams of Guinea. Revue d'Hydrobiologie Tropicale 26: 313-325.

Quist, M. C., J. S. Tillma, M. N. Burlingame, and C. S. Guy. 1999. Overwinter habitat use of shovelnose sturgeon in the Kansas River. Transactions of the American Fisheries Society 128: 522-527.

Reis, R. E., M. L. Zelditch, and W. L. Fink. 1988. Ontegenetic allometry of body shape in the neotropical catfish *Callichthys* (Teleostei: Siluriformes). Copeia 1998: 177-182.

Reyes-Gavilán, R. Garrido, A. G. Necieza, M. M. Toledo, and F. Braña. 1996. Fish community variation along physical gradients in short streams of northern Spain and the disruptive effect of dams. Hydrobiologia 321: 155-163.

Sappington, L. C., D. J. Dieterman, and D. L. Galat. 1998. Missouri River Benthic Fish Consortium 1998, standard operating procedures to evaluate the population structures and habitat use of benthic fishes along the Missouri River. Midwest Science Center, Columbia, Missouri.

Sayre, W. W., and J. F. Kennedy. 1978. Degradation and aggradation of the Missouri River. Iowa Institute of Hydraulic Research Report No. 215. The University of Iowa, Iowa City.

Scarnecchia, D. L. 1988. The importance of streamlining in influencing fish community structure in channelized and unchannelized reaches of a prairie stream. Regulated Rivers: Research and Management 2: 155-166.

Schlosser, I. J. 1985. Flow regime, juvenile abundance, and the assemblage structure of stream fishes. Ecology 66: 1484-1490.

Simberloff, D. 1972. Properties of the rarefaction diversity measurement. American Naturalist 106: 414-418.

Smith, B., and J. B. Wilson. 1996. A consumer's guide to evenness indices. Oikos 76: 70-82.

Swales, S. 1988. Fish populations of small lowland channelized river in England subject to long-term river maintenance and management works. Regulated Rivers: Research and Management 2:493-506.

Tomelleri, J. R., and M. E. Eberle. 1990. Fishes of the central United States. University Press of Kansas, Lawrence.

Vogel, S. 1981. Life in moving fluids. Princeton University Press, Princeton, New Jersey.

Weaver, L. A., and G. C. Garman. 1994. Urbanization of a watershed and historical changes in a stream fish assemblage. Transactions of the American Fisheries Society 123: 162-172.

Webb, P. W. 1975. Hydrodynamics and energetics of fish propulsion. Fisheries Research Board of Canada, Bulletin 190, Ottawa, Ontario, Canada.

Webb, P. W. 1989. Station-holding by three species of benthic fishes. Journal of Experimental Biology 145: 303-320.

Wilde, G. R., and K. G. Ostrand. 1999. Changes in the fish assemblage of an intermittent prairie stream upstream from a Texas impoundment. Texas Journal of Science 51: 203-210.

Williams, C. B. 1964. Patterns in the balance of nature. Academic Press, London.

Young, B. A., T. L. Welker, M. L. Wildhaber, C. R. Berry, and D. Scarnecchia, editors. 1997. Population structure and habitat use of benthic fishes along the Missouri and Lower Yellowstone River. 1997 Annual Report of Missouri

River Benthic Fish Study PD-95-5832 to the U. S. Army Corps of Engineers and the U. S. Bureau of Reclamation.

Zar, J. H. 1984. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.

CHAPTER 5

Habitat Use and Habitat Niche Relations for
Three Native Cyprinids in the Missouri River Hydrosystem

ABSTRACT

In the summers of 1996-1998, sampling was conducted on the Missouri and lower Yellowstone Rivers to determine if habitat changes caused by a mainstem dam have influenced niche relations among three native cyprinid species–flathead chub (*Platygobio gracilis*), sicklefin chub (*Macrhybopsis meeki*), and sturgeon chub (*Macrhybopsis gelida*). The study area was located in eastern Montana and western North Dakota and consisted of two Missouri River segments modified by a mainstem dam (segments 8 and 10) and one Yellowstone River segment (segment 9) and one Missouri River segment (segment 5), both considered quasi-natural, with few mainstem alterations. Niche relations differed among the three fish species within and among segments. In all study segments, sturgeon chub and sicklefin chub exhibited the highest niche overlap.

The most distinctive species in its habitat use was flathead chub, which was correctly classified by habitat use more than 75% of the time in each of the four segments. Sicklefin chub was the least distinctive species in its habitat use in all study segments except for segment 10. The highest niche overlap among the three species was found in segments 5 and 9 in which only 60.1% and 63.1% of individuals were correctly classified by habitat use, respectively. In segments 10 and 8, the three species exhibited the lowest niche overlap with 84.1% and 70.1% of individuals classified correctly, respectively. These results suggested that interspecific niche overlap was greater in quasi-natural segments 5 and 9 than in altered segments 8 and 10. Since segments 5 and 9 are generally environmentally less stable in summer than segments 8 and 10, these results are interpreted to

mean that environmental instability and resource partitioning interact in structuring niche relations among these three cyprinids in segments 5 and 9. Present day resource partitioning among flathead chub, sicklefin chub, and sturgeon chub in segments 8 and 10, however, may result not from competition but from a decline in the diversity of natural habitats and conditions which provided areas of overlap of habitat suitable for the three species.

INTRODUCTION

Indicator species, organisms that are closely associated with specific environmental factors (Morrison 1986), may be used as indices of environmental conditions. Criteria for selecting indicator species were proposed by Salwasser et al. (1982) to include rare and endangered species, species with specific habitat requirements, and species whose habitats and populations could be monitored to index those species with similar ecological requirements. Ideally, researchers want to monitor the population status of a few species thereby obtaining the condition of populations for all species (Block et al. 1987).

The concept of indicator species can be utilized within the framework of guilds (Block et al. 1987, Bayer and Porter 1988). A guild is comprised of species that exploit a class of environmental resources in the same or similar manner (Root 1967), or respond similarly to habitat perturbations (Szaro 1986). Effects of habitat perturbations on a single guild member can often be extrapolated to intraguild members (Bayer and Porter 1988). However, differences in resource use do occur within guilds (Block et al. 1987) and if only a single member is studied, spurious interpretation of effects of habitat perturbations on the guild can result. A more accurate or representative assessment is made with an intraguild group of species.

The modern concept of the ecological niche was given by Hutchinson (1958) as that portion of a multidimensional hypervolume occupied by a species, defined by environmental conditions under which it lives and circumscribed by competition. When two or more species use the same resource(s), competitive exclusion or

overlap of the niche results. When the latter occurs, the degree of niche overlap between or among species is proportional to the degree of competition for environmental resources (Smith 1980).

A major mechanism governing resource partitioning among stream fishes is competition (McNeely 1987). Niche distinctiveness has been used as an indicator of the importance of competition in determining resource use in fishes (Sale 1974, Pianka 1975, McNeely 1987). This approach has been criticized for lacking the rigor of experimentation (Connell 1980) however, it has been useful in descriptive studies. Several authors have shown that in unstable streams, species of minnows (Family Cyprinidae) varied in habitat use and exhibited greater niche overlap than when stable patterns of resource use were produced from competition (Harrell 1978, Mathews and Hill 1980). Stream minnows in unstable habitats may function as opportunists whose niches vary in size and structure in response to environmental change. Opportunism has been hypothesized for other organisms as well (Wiens 1974, Wiens 1976).

The Missouri River contains segments that possess severe physical and hydrologic modification and concomitant habitat loss (Hesse et al. 1989, Hesse and Sheets 1993). It has been suggested that when a resource becomes scarce animals are less selective and a resultant increase in resource use overlap among species results (Pyke et al. 1977, Krebs et al. 1983). If, in the Missouri River, physical and hydrologic changes coupled with habitat loss in modified stretches has narrowed the range and quantity of resources for native fish, increased resource and habitat use overlap could result. Other researchers, however, have found that with declining resource availability and variability a decrease in resource use overlap results among a group of organisms (Matthews and Hill 1980).

Benthic fish are a guild of fishes that exhibit similar resource use patterns (Young et al. 1997). In the upper Missouri and lower Yellowstone Rivers, three cyprinid species of an intraguild group of benthic fishes have been shown to interact ecologically and overlap to varying degrees in their resource use–flathead chub (*Platygobio gracilis*), sicklefin chub (*Macrhybopsis meeki*), and sturgeon chub

(*Macrhybopsis gelida*) (Werdon 1992, Grisak 1996, Everett 1999). These three species are common in the upper Missouri and lower Yellowstone Rivers, but have declined precipitously in abundance in the middle and lower reaches of the Missouri River. By examining niche relations within this group of fishes, the effects of habitat perturbations on the these and other native benthic fishes will be assessed.

The objectives of this study were to: 1) examine niche relations and habitat use for three native cyprinids the upper Missouri and lower Yellowstone Rivers; 2) determine if anthropogenic disturbances influence cyprinid niche relations (habitat niche overlap) in these same river reaches.

STUDY AREA

Cyprinid habitat use and niche overlap were examined in three Missouri River segments and in one Yellowstone River segment. The first segment of the Missouri River extends 111.8 km from Sturgeon Island (river km (rkm) 3141.8) in western Montana to its lower boundary of Beauchamp Coulee (rkm 3029.9) and is hereafter referred to as Missouri River Benthic Fish Study (MRBFS) segment 5 (segment 5; Figure 5.1). The second Missouri River segment is located in western Montana below Fort Peck Dam, and extends 320.3 km from Wolf Point, Montana (rkm 2737.5) to the mouth of the Yellowstone River (rkm 2546.0) and is hereafter referred to as MRBFS segment 8 (segment 8; Figure 5.1). The third Missouri River segment is located in eastern North Dakota and extends 48.3 km from the mouth of the Yellowstone River (rkm 2546) to the headwaters of Lake Sakakawea (rkm 2470.3) and is hereafter referred to as MRBFS segment 10 (segment 10; Figure 5.1). The Yellowstone River segment, hereafter referred to as MRBFS segment 9 (segment 9; Figure 5.1), extends 114.3 km from Intake Diversion Dam near Glendive (rkm 114.3) in western Montana to its mouth where it meets the Missouri River (Yellowstone River km 0.0) in western North Dakota.

The four segments exhibit differing levels of modification. Segments 5 and 9 are the least altered study segments. These segments are considered quasi-

natural because they have been subjected to few anthropogenic disturbances and are free flowing with near natural hydrographs, main channel temperatures, and turbidities. Segment 8, in contrast, is highly altered and exhibits fewer pre-impoundment physical and biological characteristics. Fort Peck Dam and Fort Peck Reservoir have created an alluvium sink which has reduced the sediment load in segment 8 causing it to be uncharacteristically clear. Furthermore, the dam regulates the hydrograph and hypolimnetic withdrawals from Fort Peck Reservoir have created cool water temperatures during the summer (Young et al. 1997). Segment 10 is less altered than segment 8. This segment has a semi-natural hydrograph, a result of the merging of the free-flowing Yellowstone River and the Missouri River (segment 8) which is regulated upstream by Fort Peck Dam. During the present study, main channel water temperatures in segment 10 were 3-5 °C warmer in summer than those in nearby segment 8. Segment 10 is also characterized by high main channel turbidity, no major shoreline development, and few revetment banks (rip-rap). As with segments 5 and 9, the lack of shoreline development and revetment banks allows the main river channel to meander naturally which creates a diversity of off-channel habitats.

METHODS

Data Collection

Data for this research were obtained from Missouri River Benthic Fish Study (MRBFS) data collected in 1996, 1997, and 1998. A stratified random sample was used to collect fish in the three study segments where the strata were macrohabitat types. These macrohabitats were main channel cross-over, outside bend, inside bend, secondary channel: non-connected, secondary channel: connected, tributary mouth (Figure 5.2). In the segments, macrohabitats served as sampling units. In each segment, fish were collected from five randomly selected sample units of each stratum from July through September in both 1996, 1997, and 1998. A variety of fish capturing gears were used that would effectively sample the great variety of

depths and velocities within habitats, thereby ensuring accurate description of each species' habitat use. These gears were a bag seine (10.7 m long, 1.8 m high, 1.8 m^3 bag, 5 mm mesh), a benthic beam trawl (2 m wide, 0.5 m high, 5.5 m long, 3.2 mm inner bag mesh), a trammel net (22.9 m long, inner wall 2.4 m deep with 2.5 cm mesh, outer wall 1.8 m deep with 20.3 cm mesh), an electrofishing boat (Coffelt VVP-15 variable voltage pulsator, 5,000 W generator), and a gill net (30.5 m long, 1.8 m high, mesh sizes of 1.9 cm, 3.8 cm, 5.1 cm, 7.6 cm). Gear selectivity and efficiency bias may have existed but were not addressed empirically. For individual fish, total length (mm) and weight (g) were obtained for each species. A subsample was a single gear sample.

Water depth (m), velocity (m/sec), temperature (°C), turbidity (Nephalometric Turbidity Units; NTU), and substrate (% silt, % sand, % gravel) were measured at each subsample following the successful deployment and retrieval of fish collecting gears and later used to characterize segments and segment macrohabitats. For an in-depth description of habitats, measurement of habitat physiochemical variables, and fish collection techniques, see Sappington et al. (1998). In macrohabitat replicates greater than 1.5 m in depth, a boat was anchored at the proper location and water depth was measured with a Lowrance sonar device to the nearest 0.1 m. Current velocity was measured with the aid of an A55M sounding reel and hangar bar (19.1 mm x 304.8 mm). A Marsh-McBirney Flowmate Model 2000 probe was attached to the hangar bar and lowered 0.8 of the water column depth with the sounding reel. A 22.7 kg sounding weight was used to keep the current velocity meter probe pointed into the current and positioned directly below the boat. Current velocity was measured to the nearest 0.1 m/sec.

Water temperature was measured with a YSI 30 temperature/conductivity meter. The meter probe was held 1-2 feet under the water's surface and temperature was measured to the nearest 0.1 °C. A vial sample was collected approximately 0.5 m below the water's surface and the turbidity of the sample was measured with a Hach 2100P turbidity meter to the nearest 1.0 NTU.

A bottom substrate sample was collected with an iron pipe that had one end closed. One end of a nylon rope was attached to the open end of the pipe and the other connected to the boat. The pipe was then dragged through the area of the gear sample. The pipe contents were emptied onto the boat and the percentage of silt (particle size <= 0.06 mm), sand (particle size 0.06 <= 2.0 mm), and gravel (particle size 2.0 mm <= 16 mm) were visually estimated. Later, the geometric mean of substrate size was calculated for each subsample (McMahon et al. 1997).

Velocity, turbidity, temperature, and substrate were also measured with the same devices in shallow macrohabitat replicates at each fish collection subsample. Water column depth and water velocity were measured with the aid of a standard wading rod at three points along the gear sampling area. A substrate sample was collected with the iron pipe by dragging it along the area sampled by the fish collecting gear. Percentages of sand, silt, and gravel were then estimated from the pipe's contents.

Daily discharge mean and variability (as expressed by coefficient of variation) for each segment was determined for twelve months and for the three month study period and averaged to obtain the three year average for each. Daily discharge data were obtained from the United States Geological Survey webpage (www.waterdata.usgs.gov/nwis-w/mt.).

Analyses

Segment and Habitat Characterization

Distinctiveness of macrohabitats among segments was evaluated with a multivariate technique. Multivariate analysis of variance (MANOVA; Johnson and Wichern 1992) was conducted across segments and macrohabitat types, with segment x macrohabitat combinations serving as the independent variable and water physiochemical categories serving as the dependent variable (depth, current velocity, turbidity, temperature, percent silt, percent sand).

$$(5.1) \quad Y_{rij} = \mu + \tau_i + \beta_j + \gamma_{ij} + e_{ijr}$$

$$i = 1, 2, \ldots, g$$

$$j = 1, 2, \ldots, b$$

$$r = 1, 2, \ldots, n$$

where Y_{rij} = is the rth physiochemical variable value for macrohabitat i in segment j, μ = overall mean (level), T_i = the macrohabitat i effect, βj = the segment j effect, Y_{ij} = interaction between macrohabitats and segments, e_{ijr} are independent, normally distributed variables, g = number of macrohabitats, b = number of segments, and n = number of physiochemical categories.

The hypotheses used for MANOVA testing are as follows:

H_o= $Y_{11} = Y_{21} = \ldots Y_{ik} = 0$ (there is no difference in physiochemical characteristics among macrohabitats across segments).

H_A=   at least one $Y_{ik} \neq 0$

The equal variance-covariance assumption was checked with the Box test (Box 1949) and residual plots for each dependent variable was constructed to examine homoscedasticity. Multicollinearity between dependent variables was examined by computing the variance inflation factor. An appropriate transformation, such as arcsine (square root (y)), log (y+1), or square root (y), was applied to dependent variables that violated any of the assumptions (Hair et al. 1995).

Canonical analysis of variates followed a significant MANOVA (Johnson and Wichern 1992). Canonical analysis of variates assessed the composite relationship between multiple dependent and multiple independent variables. Through this procedure, weighted, linear composites of dependent variables (water physiochemical categories), called canonical variables, were derived that maximized the difference between the independent variables (segment x macrohabitat combinations). Those dependent variables with the highest correlations with the first canonical variable contributed most to the separation of segment macrohabitats, as the first canonical variable defined the greatest separation (Johnson and Wichern 1992). Mean canonical variables scores for segment macrohabitats were plotted to examine segment differences for each macrohabitat type.

For the MANOVA, the null hypothesis tested was the equality of vectors of means of multiple dependent variables (water physiochemical variables) across study segments. Klecka (1975) concluded that this multivariate technique was

robust enough that the assumptions of a multivariate normal distribution of discriminating variables and equal variance-covariance matrices between groups need not be rigorously met. The data were analyzed using the Statistica (Statsoft Inc. 1997) software package.

Analysis of variance (ANOVA) procedures were used to further interpret the canonical analysis of variates results.

$$(5.2) \quad Y_{ijk} = \mu + \alpha_j + \beta_k + (\alpha\beta)_{jk} + \varepsilon_{ijk}$$

$$i = 1, 2, \ldots, g$$

$$j = 1, 2, \ldots, n$$

$$k = 1, 2, \ldots, b$$

where Y_{ijk} = is a physiochemical value for observation i for macrohabitat k in segment j, μ = overall mean (level), α_j = the segment j effect, β_k = macrohabitat k effect, $(\alpha\beta)_{jk}$ = interaction between segments and macrohabitats, ε_{ijk} = the error effect associated with Y_{ijk} which is normally distributed, g = number of observations, n = number of segments, and b = number of macrohabitats.

The hypotheses used for ANOVA testing are as follows:

$H_o=$ $(\alpha\beta)_{11} = (\alpha\beta)_{21} = \ldots(\alpha\beta)_{jk} = 0$ (there is no difference in the physiochemical variable among macrohabitats across segments).

$H_A=$ at least one $(\alpha\beta)_{jk} \neq 0$

The assumptions of a normal distribution and homogeneity of variance were examined prior to the ANOVA. A one-way ANOVA was performed on each habitat variable (depth, velocity, turbidity, temperature, % sand, % silt). If the F-test for segment and macrohabitat effects was significant this would indicate that the water physiochemical variable is different for macrohabitats among the segments, aiding in the interpretation of which physiochemical variables are responsible for segment x macrohabitat differences in the canonical analysis. The data were analyzed using the SAS (SAS Institute 1990) software package.

Habitat Use

The relative abundance of the three cyprinid species (flathead chub, sicklefin chub, sturgeon chub) was determined for each macrohabitat in each segment by

dividing the total number of fish of a species captured in that macrohabitat by the total number of fish of that species captured in that segment. This ratio was computed for each year and then averaged across years to obtain the three year average for each macrohabitat.

Categorical data modeling was also used to determine segment and macrohabitat utilization. The data were analyzed in a two-dimensional contingency table. The rows corresponded to macrohabitats (independent variables). The two columns of the table represented the number of macrohabitat sample units in which the fish species was either present or absent (dependent variables). The frequency in the (i,j)th cell is the number of fish in the ith macrohabitat that have the jth response (presence or absence). For the sample i, the probability of the jth response (π_{ij}) is estimated by the sample proportion, $p_{ij} = n_{ij}/n_i$ (n is the macrohabitat type). The vector (**p**) of all such proportions is then transformed into a vector of functions, denoted by **F**=**F(p)**. If π denotes the vector of true probabilities for the entire table, then the functions of true probabilities, denoted by **F(π)**, are assumed to follow a linear model.

(5.3) $\mathbf{E_A(F) = F(\pi) = X\beta}$

where $\mathbf{E_A}$ denotes asymptotic expectation, **X** is the design matrix containing fixed constants, and β is a vector of parameters to be estimated.

This procedure was used to test the null hypothesis that habitat use of each cyprinid species did not differ among the four segments. Through this analysis, log-linear models were fit to functions of species presence (1) and absence (0) frequencies. This analysis used maximum-likelihood estimation of parameters for the models. A Chi-square statistic (χ^2) was used to test for a significant difference in partitioning of variance among the response functions (presence or absence) (SAS 1990). Differences in segment and macrohabitat use for each species was examined. Simple effects contrasts were used to further interpret macrohabitat use differences among segments for a species (Kirk 1995).

Distinctiveness of fish species habitat use among segments was determined with a multivariate technique. Multivariate analysis of variance (MANOVA) was

conducted across segments and species, with segment x species combinations serving as the independent variable and water physiochemical categories serving as the dependent variable (depth, current velocity, turbidity, temperature, % silt, % sand).

$$(5.4) \quad Y_{rij} = \mu + T_i + \beta_j + \gamma_{ij} + e_{ijr}$$

$$i = 1, 2, \ldots, g$$

$$j = 1, 2, \ldots, b$$

$$r = 1, 2, \ldots, n$$

where Y_{rij} = is the rth physiochemical variable value for species i in segment j, μ = overall mean (level), T_i = the species i effect, β_j = the segment j effect, γ_{ij} = interaction between segments and species, e_{ijr} are independent, normally distributed variables, g = number of species, b = number of segments, and n = number of physiochemical categories.

The hypotheses used for MANOVA testing are as follows:

$H_o=$ $\quad \gamma_{11} = \gamma_{21} = \ldots \gamma_{ik} = 0$ (there is no difference in physiochemical variable use among species across segments).

$H_A=$ $\quad$ at least one $\gamma_{ik} \neq 0$

The equal variance-covariance assumption was checked with the Box test (Box 1949) and residual plots for each dependent variable was constructed to examine homoscedasticity. Multicollinearity between dependent variables was examined by computing the variance inflation factor. An appropriate transformation, such as arcsine (square root (y)), log (y+1), or square root (y), was applied to dependent variables that violated any of the assumptions (Hair et al. 1995). Canonical analysis of variates followed a significant MANOVA. Mean canonical variables scores for species habitat use were determined for each segment and plotted to examine differences among segments. Analysis of variance (ANOVA) procedures were used to further interpret the canonical analysis of variates results.

$$(5.5) \quad Y_{kij} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + e_{ijk}$$

$$i = 1, 2, \ldots, g$$

$$j = 1, 2, \ldots, n$$

$$k = 1, 2, \ldots, b$$

where Y_{kij} = is the kth physiochemical variable value for species i in segment j, μ = overall mean (level), α_i = the species i effect, β_j = the segment j effect, $(\alpha\beta)_{jk}$ = interaction between species and segments, e_{ijk} = the error effect associated with Y_{ijk} that is normally distributed, g = number of species, n = number of segments, and b = number of physiochemical categories.

The hypotheses used for ANOVA testing are as follows:

H_o= $(\alpha\beta)_{11} = (\alpha\beta)_{21} = \ldots(\alpha\beta)_{jk} = 0$ (there is no difference in the use of the physiochemical variables among species across segments).

H_A= at least one $(\alpha\beta)_{jk} \neq 0$

ANOVA assumptions were checked as described for the segment x macrohabitat analysis. The data were analyzed using the SAS (SAS Institute 1990) software package.

Habitat Niche Overlap

Habitat niche distinctiveness of each species within each segment was examined by discriminant analysis and classification (Johnson and Wichern 1992). Group membership was defined by species and independent variables were scores on each physiochemical variable taken from a macrohabitat subsample in which at least one individual of a species was found. Discriminant analysis was used to derive new variables that best described species habitat use differences. Classification was used to assess the predictive accuracy of the results obtained from discriminant analysis.

Both discriminant analysis and classification have been used to describe niche relations among fish species (Baker and Ross 1981, McNeely 1987). For discriminant analysis, an omnibus MANOVA was used to test the null hypothesis that no significant difference in resource use existed among species in a segment.

(5.6) $Y_{ir} = \mu + T_i + e_{ir}$

$i = 1, 2, \ldots, g$

$r = 1, 2, \ldots, n$

where Y_{ir} = physiochemical category r used by cyprinid species i, μ = overall mean (level), T_i = the cyprinid species i effect, e_{ir} are independent, normally distributed variables, g = number of cyprinid species, and n = number of physiochemical categories used by cyprinid species i.

The hypotheses used for MANOVA testing are as follows:

H_o= $T_1 = T_2 = \ldots T_g = 0$ (there is no difference in habitat use among cyprinid species).

H_A=   at least one $T_i \neq 0$

Following a significant MANOVA, pairwise comparison of species habitat use was made with Hotelling's T^2 (Johnson and Wichern 1992). The discriminant analysis for each segment derived canonical variables, each representing a difference in habitat use (physiochemical variable use) among the three cyprinid species. Plots of species positions on the first two canonical variables gave an indication of niche overlap or distinctiveness among the three cyprinids. Niche overlap was also inferred with classification analysis. Misclassification of a cyprinid species occurred because the individual was similar to another species in its resource use and was assigned incorrectly to this species. The more misclassifications that occurred, the more alike the two species were in their resource use (McNeely 1987). Therefore, in this study, niche overlap was treated as analogous to percent miclassification (Baker and Ross 1981).

For discriminant analysis, the equal variance-covariance assumption was checked with the Box test (Box 1949) and residual plots for each dependent variable was constructed to examine homoscedasticity. Multicollinearity between dependent variables was examined by computing the variance inflation factor. An appropriate transformation, such as arcsine (square root (y)), log (y+1), or square root (y), was applied to dependent variables that violated any of the assumptions (Hair et al. 1995).

Discriminant analysis is sufficiently robust that the multivariate normal distribution assumption and the equal variance-covariance matrices between groups assumption need not be rigorously met (Klecka 1975).

RESULTS

Physical Characteristics of Segments and Habitats

Below dam segments 8 and 10 had greater depths, lower temperatures, and finer substrates than quasi-natural segments 5 and 9 (Tables 5.1-5.4). Segment 5 exhibited the lowest turbidities among the segments. No velocity pattern among segments was observed.

Mean daily three month and twelve month discharge increased down river. Segment 5 had the lowest mean three month discharge (318.7 m^3/sec) and twelve month discharge (294.8 m^3/sec) (Table 5.5). Segment 10 had the highest three month discharge (813.8 m^3/sec) and twelve month discharge (856.5 m^3/sec). Variability (as expressed by coefficient of variation) in twelve month and three month daily discharge was highest for segments 5 (three month=53.4, twelve month=65.7) and 9 (three month=65.0, twelve month=86.5) and lowest for segment 8 (three month=27.0, twelve month=30.1) (Table 5.5).

Within the four segments, main channel cross-over and outside bend macrohabitats tended to exhibit greater depths, velocities, and coarser substrates than other macrohabitats (Tables 5.1-5.4). Secondary channel: non-connected macrohabitat tended to exhibit lower depths and velocities and finer substrates than other macrohabitats in all four segments. This habitat also had the highest water temperatures. The macrohabitats with the highest and lowest turbidities varied among the segments.

Macrohabitat physiochemical differences existed among segments (MANOVA, Wilk's lambda=0.5434, $P<0.0001$). The canonical analysis of macrohabitats derived five canonical variables, each a composite of physiochemical variables (Table 5.6). The first two variables accounted for approximately 74% of the macrohabitat differences among segments. Depth exhibited the largest score (standardized canonical coefficient) on the first canonical variable (1.2512) which

indicated that this variable was responsible for most of the macrohabitat differences among the four segments.

Mean scores for canonical variable one plotted across macrohabitat types indicated that segment 10 main channel cross-over and inside bend macrohabitats and segment 5 outside bend macrohabitat were most responsible for differences among segment macrohabitats (Figure 5.3). Mean scores were similar for the other four macrohabitat types among the four segments.

Habitat Use

A total of 10,431 flathead chub (segment 5=2,856; segment 8=315; segment 9=6,393; segment 10=867), 416 sicklefin chub (segment 5=239; segment 8=52; segment 9=74; segment 10=51), and 1,360 sturgeon chub (segment 5=365; segment 8=133; segment 9=801; segment 10=61) was sampled from the four segments. Ninety-two percent of flathead chub were captured with the bag seine, whereas 100% of sicklefin chub and 95% of sturgeon chub were captured with the benthic trawl. Among the four segments, most flathead chub (67-91%) were captured in inside bend and secondary channel: connected macrohabitats which tended to exhibit shallow depths and low to medium current velocities (Table 5.7). In most segments, sturgeon chub catch and sicklefin chub catch were distributed nearly evenly among main channel cross-over, inside bend, outside bend, and secondary channel: connected macrohabitats. Seventy-three to one-hundred percent of sturgeon chub and ninety-five to one-hundred percent of sicklefin chub were captured in these four macrohabitat types (Table 5.7). These habitats exhibited a variety of depths and velocities.

Flathead chub tended to use shallower depths, lower current velocities, and finer substrates than sturgeon chub or sicklefin chub (Tables 5.8-5.10). Turbidities and temperatures at capture sites for all three species were similar among the four segments. The three species used finer substrates, characterized by more sand and less gravel, in segments 8 and 10 than in segments 5 and 9. Sicklefin and sturgeon chub tended to use slightly higher current velocities in segments 8 and 10 than in segments 5 and 9 (Tables 5.8-5.10).

Macrohabitat use differed significantly among the four segments for flathead chub (categorical data modeling, segment x macrohabitat interaction, χ^2=29.10, P=0.0038), but not for sicklefin chub (χ^2=14.94, P=0.22) and sturgeon chub (χ^2=10.12, P=0.61) (Table 5.11). Use of inside bend (χ^2=11.02, P=0.01), outside bend (χ^2=13.46, P=0.0037), and secondary channel: non-connected (χ^2=11.53, P=0.0092) macrohabitats differed among the four segments for flathead chub and were responsible for the significant interaction (Table 5.12).

Habitat use differences existed among the three species among segments (MANOVA, Wilk's lambda=0.8886, P<0.0001). The canonical analysis of habitat use derived three canonical variables, each a composite of physiochemical variables (Table 5.13). The first two variables accounted for approximately 97% of the habitat use differences among segments. Depth exhibited the largest score (standardized canonical coefficient) on the first canonical variable (1.0697) which indicated that this variable was responsible for most of the habitat use differences.

Mean scores for canonical variable one plotted across segments and species indicated that habitat use was similar for flathead chub among segments and that sicklefin chub and sturgeon chub habitat use were most responsible for differences among segments. Mean canonical scores for the three species were most similar in segments 5 and 9 and least similar in segments 8 and 10 (Figure 5.4). Mean scores for sicklefin and sturgeon chub were similar to each other in all segments, but flathead chub scores were much lower. Similarity in habitat use thus existed between sicklefin and sturgeon chub but not between between flathead chub and either of the other two species.

Habitat Niche Overlap

Habitat use differences existed among the three cyprinid species (MANOVA; segment 5, Wilk's lambda=0.7316, P<0.0001; segment 8, Wilk's lambda=0.4766, P<0.0001; segment 9, Wilk's lambda=0.6323, P<0.0001; segment 10, Wilk's lambda=0.2375 P<0.0001) in each river segment. Between species pairs, habitat use differed significantly between flathead chub and both sicklefin and sturgeon chub (Hotelling's T^2, P<0.05) in all segments (Table 5.14). Habitat use differed

significantly between sicklefin and sturgeon chub only in segment 10. Discriminant analysis of cyprinid habitat use in each of the four segment derived two canonical variables, each a composite of the physiochemical categories retained (Table 5.15). The first canonical variable accounted for 89-99% of the habitat use differences among the three species in any one segment. Current velocity exhibited the largest score (standardized canonical coefficients) on the first canonical variable (current velocity; segment 5= 0.5631, segment10= -0.6914) in segments 5 and 10 which indicated that current velocity was responsible for most of the habitat use differences among the three species in each of these segments (Table 5.15). Depth exhibited the largest score (standardized canonical coefficients) on the first canonical variable (depth; segment 8= -0.6300, segment 9= 0.7737) in segments 8 and 9 which indicated that this variable was most responsible for habitat use differences in these segments.

Plots of individual scores on the two canonical variables resulted in varying degrees of overlap among the three species habitat use in each of the four segments (Figures 5.5-5.8). In all study segments, sturgeon chub and sicklefin chub exhibited the highest niche overlap between any two species. In segment 5, flathead chub, sicklefin chub, and sturgeon chub (in that order) showed progressively decreasing use of shallow, low velocity sites with fine substrate and increasing use of deep, high velocity sites with coarse substrate (Figure 5.5). In segment 8, flathead chub, sicklefin chub, and sturgeon chub (in that order) showed progressively decreasing use of deep, high current velocity sites with coarse substrate and increasing use of shallow, low current velocity sites with fine substrate (Figure 5.6). Flathead chub, sicklefin chub, and sturgeon chub showed the preceding order of decreasing use of deep sites with coarse substrate and increasing use of shallow sites with fine substrates in segment 9 (Figure 5.7). In segment 10, the three species exhibited a pattern similar to that found in segment 8 (Figure 5.8). Overall, niche overlap for the three species was highest in segment 5 and 9 and lowest in segments 8 and 10.

The species that was most distinctive in its habitat use was flathead chub which was correctly classified by habitat use over 75% of the time in each of the four segments. Sicklefin chub was the least distinctive species in all study segments except segment 10 (Table 5.16). The highest niche overlap among the three species was found in segments 5 and 9 in which only 60.1% and 63.1% of individuals were correctly classified, respectively. In segments 10 and 8, the three species exhibited the lowest niche overlap with 84.1% and 70.1% of individuals classified correctly, respectively (Table 5.16). The higher niche overlap in segments 5 and 9 than in segments 8 and 10 may be related to higher overlap between flathead chub and the remaining species. Flathead chub was misclassified (by percentage) as sturgeon chub (segment 5=50.0%, segment 9=26.2%) and sicklefin chub (segment 5=49.3%, segment 9=10.0%) most often in segments 5 and 9 (Table 5.16). Flathead chub was classified correctly most often in segment 10 (96.0%) and least often as sicklefin chub (0.0%) and sturgeon chub (12.2%) in segments 10 and 8, respectively.

DISCUSSION

Habitat Use

Differences in habitat use between flathead chub and both sturgeon chub and sicklefin chub are consistent with results reported elsewhere. For example, I found that flathead chub used shallower, slower-moving water, whereas sicklefin chub sturgeon chub both used habitats that were deeper and faster moving. Grisak (1996) collected most flathead chub from shallow peripheral zone habitat (mean depth=0.58 m, mean velocity=0.32 m/sec) and most sicklefin and sturgeon chub from deep-water zone habitat (mean depth=2.94 m, mean velocity=0.61 m/sec) in the Missouri River, Montana. In smaller rivers and streams, however, Werdon (1992) reported that flathead chub and sturgeon chub utilized similar shallow-water habitat. Although some sturgeon chub were captured in shallow, low velocity habitat in this study, most were captured in deep habitat with high velocities. Deep habitats

with high velocities were probably absent in smaller streams considered by Werdon (1992).

In the upper Missouri and lower Yellowstone Rivers, Everett (1999) found that habitat use differed significantly between sicklefin and sturgeon chub with sturgeon chub using faster, deeper water with coarser substrate than sicklefin chub, which contradicts findings in this study for depth and velocity utilization. Like Everett (1999), this study found that sturgeon chub used coarser substrate than sicklefin chub. Perhaps sturgeon chub can survive in habitats that exhibit a variety of depths and velocities, but coarse substrate is essential for survival. Substrate may be the most important habitat variable within a particular range of depths and velocities and sturgeon chub favor habitat with coarse substrate within this range.

Habitat Niche Overlap

Main channel habitats (main channel cross-over, outside bend, inside bend, and secondary channel: connected) in quasi-natural segments 5 and 9 were shallower and exhibited lower velocities than altered segments 8 and 10. Above segments 8 and 10, Fort Peck Dam acts as a sediment trap, preventing downstream transport of sediment from upper reaches and results in downcutting and deepening of the main channel and its habitats (Leopold et al. 1964). Before mainstem alteration, the Missouri River channel was characterized by a high diversity of depths and velocities (Hesse and Sheets 1993). Today the main channel in many altered river sections has been converted into a trapezoidal shape, leaving the main channel devoid of habitats characterized by shallow and intermediate depths and low velocities.

Fort Peck Dam also influences the river hydrograph in segments 8 and 10. After closure of Fort Peck Dam in 1940, mean monthly discharge has increased from its historical level by as much as 404 m³/sec in February and decreased by as much as 614 m³/sec in June. The dam has also lowered flow variability in below dam river segments (Hesse and Sheets 1993). Variability in daily flow was much lower in below-dam segments 8 and 10 then in segments 5 and 9 in this study. During summer, river discharge can increase or decrease by as much as 50 percent

over a seven-day period in segments 5 and 9. Flow changes of this magnitude are virtually absent in altered segments 8 and 10 during this time period.

Differences in the physical characteristics between segments 5 and 9 and segments 8 and 10 can be attributed to Fort Peck Dam. Segment differences in habitat niche overlap among flathead chub, sicklefin chub, and sturgeon chub may be associated with loss of main channel habitats that are characterized by shallow and intermediated depths and low velocities. In the present study, sicklefin and sturgeon chub exhibited high overlap in their use of deep, high velocity habitat in all study segments. Everett (1999) also found that sicklefin and sturgeon chubs were frequently captured together in habitats that were deep and exhibited high current velocities. Most differences between segments 5 and 9 and segments 8 and 10 in habitat niche overlap among the three species resulted from habitat use differences between flathead chub and sturgeon chub, not between either of these two species and sicklefin chub. In quasi-natural segments 5 and 9, sturgeon chub and flathead chub exhibited higher overlap in their use of shallow, low velocity habitat than was exhibited between the two species in altered segments 8 and 10. Werdon (1992) also found that flathead chub and sturgeon chub overlapped in their use of this habitat. A loss of shallow habitats that provided conditions suitable for both flathead chub and sturgeon chub would cause a decrease in overlap between these two species. A loss of shallow, low velocity habitats from downcutting of the main channel in segments 8 and 10 would explain the low habitat niche overlap found between sturgeon chub and flathead chub in these altered segments.

High flow variability has been shown to influence niche relations among fishes in small streams. McNeely (1987) hypothesized that in upstream reaches of an Ozark stream high niche overlap within a cyprinid community was related to high flow variability and high fluctuation of other environmental variables and that niche overlap was lower among cyprinids in the more environmentally stable lower reaches. Further, McNeely (1987) determined that high environmental stability allowed competition to shape resource use among stream cyprinids in the absence of high environmental instability. A similar hypothesis was suggested by Schlosser

(1982). An absence of high environmental instability in altered segments 8 and 10 resulting from a dam controlled hydrograph, may have allowed competition to reduce niche overlap among the three cyprinid species. In the present study, however, insufficient information exists to determine if competition plays a role in shaping resource use among sicklefin chub, sturgeon chub, and flathead chub.

LITERATURE CITED

Baker, J. A., and S. T. Ross. 1981. Spatial and temporal resource utilization by southeastern cyprinids. Copeia 1981: 178-189.

Bayer, M., and W. F. Porter. 1988. Evaluation of a guild approach to habitat assessment for forest-dwelling birds. Environmental Management 12: 797-801.

Block, W. M., L. A. Brennan, and R. J. Gutierrez. 1987. Evaluation of guild-indicator species for use in resource management. Environmental Management 11: 265-269.

Box, G. E. P. 1949. A general distribution theory for a class of likelihood criteria. Biometrika 36: 317-346.

Connell, J. H. 1980. Diversity and coevolution of competitors, or the ghost of competition past. Oikos 35: 131-138.

Everett, S. R. 1999. Ecology and life history of three native benthic fishes in the Missouri and Yellowstone River. Master's thesis. University of Idaho, Moscow.

Giller, P. S. 1984. Community structure and the niche. Chapman and Hall, New York.

Grisak, G. G. 1996. The status and distribution of the sicklefin chub in the middle Missouri River, Montana. Master's thesis. Montana State University, Bozeman.

Hair, J. F., Jr., R. E. Anderson, R. L. Tatham, and W. C. Black. 1995. Multivariate data analysis with readings. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.

Harrell, H. L. 1978. Response of the Devil's River (Texas) fish community to flooding. Copeia 1978: 60-68.

Hesse, L. W., J. C. Schmulbach, J. M. Carr, K. D. Keenlyne, D. G. Unkenholz, J. W. Robinson, and G. E. Mestl. 1989. Missouri River fishery resources in relation to past, present, and future stresses. Pages 352-371 *in* D. P. Dodge, editor. Proceedings of the International Large River Symposium. Canadian Special Publications of Fisheries and Aquatic Science, 106, Ottawa, Ontario, Canada.

Hesse, L. W., and W. Sheets. 1993. The Missouri River hydrosystem. Fisheries 18(5): 5-14.

Hutchinson, G. E. 1958. Concluding remarks. Cold Spring Harbor Symposia. Quantitative Biology 22: 415-427.

Johnson, R. A., and D. W. Wichern. 1992. Applied multivariate statistical analysis. Prentice Hall, New Jersey.

Kirk, R. E. 1995. Experimental design: procedures for the behavioral sciences. Brooks/Cole Publishing Co., Pacific Grove, California.

Klecka, W. H. 1975. Discriminant analysis. Page 435 *in* N. H. Nie, C. H. Hall, T. G. Jenkins, K. Steinbrenner, and D. H. Brent, editors. Statistical Package for the Social Sciences, 2nd edition. McGraw-Hill, New York.

Krebs, J R., D. W. Stephens, and W. J. Sutherland. 1983. Perspectives in optimal foraging *in* A. H. Brush and G. A. Clark, Jr., editors. Perspectives in Ornithology. Cambridge University Press, Cambridge, U. K.

Leopold, L. B., M. G. Wolman, and J. P. Miller. 1964. Fluvial processes in geomorphology. W. H. Freeman, San Francisco, California.

Matthews, W. J., and L. G. Hill. 1980. Habitat partitioning in the fish community of a southwestern river. The Southwestern Naturalist 25: 51-66.

McMahon, T. E., A. V. Zale, and D. J. Orth. 1997. Aquatic habitat evaluation. Pages 83-120 *in* B. R. Murphy and D. W. Willis, editors. Fisheries Techniques, Second Edition. American Fisheries Society, Bethesda, Maryland.

McNeely, D. L. 1987. Niche relations within an Ozark stream assemblage. Environmental Biology of Fishes 18: 195-208.

Morrison, M. L. 1986. Bird as indicators of environmental change. Pages 429-451 *in* R. J. Johnston, editor. Current ornithology, volume 3. Plenum, New York.

Pianka, E. R. 1975. Niche relations of desert lizards. Pages 292-314 *in* M. Cody and J. Diamond, editors. Ecology and Evolution of Communities. Belknap Press, Cambridge, Massachusetts.

Pyke, G. H., H. R. Pulliam, and E. L. Charnov. 1977. Optimal foraging: a selective review of theory and test. The Quarterly Review of Biology 52: 137-154.

Root, R. B. 1967. The niche exploitation pattern of the blue-gray gnatcatcher. Ecological Monographs 37: 317-350.

Sale, P. F. 1974. Overlap in resource use and interspecific competition. Oecologia 37: 245-256.

Salwasser, H., I. D. Luman, and D. Duff. 1982. Integrating wildlife and fish into public land forest management. Proceedings of the Western Association of Fish and Wildlife Agencies 62: 293-299.

Sappington, L. C., D. J. Dieterman, and D. L. Galat. 1998. Missouri River Benthic Fish Consortium 1998 standard operating procedures to evaluate the population structures and habitat use of benthic fishes along the Missouri River. Midwest Science Center, Columbia, Missouri.

SAS. 1990. SAS System. SAS Institute Inc., Cary, North Carolina.

Schlosser, I. J. 1982. Fish community structure and function along two habitat gradients in a headwater stream. Ecological Monographs 52: 395-414.

Smith, R. L. 1980. Ecology and field biology, 3rd edition. Harper and Row, New York.

Statsoft, Inc. 1997. Statistica User's Guide. 1997 edition. Statsoft Inc., Tulsa, Oklahoma.

Szaro, R. C. 1986. Guild management: an evaluation of avian guilds as a predictive tool. Environmental Management 10: 681-688.

Wiens, J. A. 1974. Climatic instability and the 'ecological saturation' of bird communities in North American grasslands. The Condor 76: 385-400.

Wiens, J. A. 1976. Population responses to patchy environments. Annual Review of Ecology and Systematics 7: 81-120.

Werdon, Selena J. 1992. Population status and characteristics of *Macrhybopsis gelida, Platygobio gracilis*, and *Rhinichthys cataractae* in the Missouri River Basin. Master's thesis. South Dakota State University, Brookings.

Young, B. A., T. L. Welker, M. L. Wildhaber, C. R. Berry, and D. Scarnecchia, editors. 1997. Population structure and habitat use of benthic fishes along the Missouri and Lower Yellowstone River. 1997 Annual Report of Missouri

River Benthic Fish Study PD-95-5832 to the U. S. Army Corps of Engineers and the U. S. Bureau of Reclamation.

CONCLUSION

It was concluded (in Chapters 2-5) that habitat changes in segments of the Missouri River have altered the fish community composition and the ecology of many native fish species. Many of these conclusions were arrived at through complex statistical analyses. Strong evidence linking river alteration to changes in the native fish community can be found in the state of North Dakota in the two North Dakota segments (segments 10 and 12, Chapter 4, Figure 4.1). The segments are separated by Garrison Dam and 286.5 km of impounded Missouri River (Lake Sakakawea). Prior to the closure of Garrison Dam (in December 1953), these two river segments were connected and probably contained very similar fish communities. Today, these two segments exhibit greatly different physical characteristics and fish communities.

Segment 10 is considered pseudo-natural as it retains some natural Missouri River characteristics. This segment is free-flowing with a semi-natural hydrograph, a result of the merging of the free-flowing Yellowstone River and the Missouri River, which is regulated upriver by Fort Peck Dam. This segment is also characterized by high main channel turbidity, no major shoreline development, and few revetment banks (rip-rap). The lack of shoreline development and revetment banks allows the main river channel to meander naturally, which creates a diversity of off-channel habitats.

Segment 12, in contrast, is a highly altered segment and exhibits fewer pre-impoundment physical and biological characteristics. Garrison Dam and Lake Sakakawea have created an alluvium sink, thereby reducing the sediment load in the river below the dam. The river below the dam is uncharacteristically clear and natural aggradative and degradative processes have been disrupted. The dam strongly regulates the hydrograph. Furthermore, hypolimnetic withdrawals from Lake Sakakawea have created uncharacteristically cool water temperatures during the summer with maximum summer temperatures approximately 9 °C cooler than before impoundment (Chapter 4, page 81). This segment is also characterized by numerous revetments and a high degree (25-40%) of shoreline development and bank stabilization (Chapter 4, page 81).

The fish communities of the two segments differed greatly. Small native minnows (Cyprinidae), particularly flathead chub (*Platygobio gracilis*; Table 4.1), were common in segment 10 in 1997 and 1998, constituting 55% of the fish there

(Table 4.2). Three other native minnow species, sicklefin chub (*Macrhybopsis meeki*), sturgeon chub (*Macrhybopsis gelida*), and western silvery minnow (*Hybognathus argyritis*), were also frequently captured in segment 10 (Chapter 3, Table 3.2; segment 10 referred to as below confluence segment). In segment 12, minnows constituted only 3% of the fish (Table 4.2). No flathead chub, sicklefin chub, sturgeon chub, or western silvery minnow were captured in segment 12. Native deep-bodied suckers such as bigmouth buffalo (*Ictiobus cyprinellus*) and smallmouth buffalo (*Ictiobus bubulus*) (Catostomidae; 17%) were common in segment 10 (Chapter 4, Table 4.1) however, native suckers were nearly absent from segment 12. The fish community in segment 12 was dominated by two suckers, white sucker (*Catostomus commersonii*) and longnose sucker (*Catostomus catostomus*), which represented 91% of the fish catch (Chapter 4, Table 4.3). These two species are not considered to be members of the native Missouri River fish fauna and are most often found in rivers and streams that are characterized by cool water temperatures and low turbidities (Chapter 2, page 29).

The very different fish communities in segments 10 and 12, strongly suggests that habitat alterations, such as those caused by mainstem dams, have had a significant impact on the native Missouri River fish fauna. Natural river conditions, such as those found in segment 10, appear to be essential for sustainable populations of many native Missouri River fishes.

APPENDIX A. FIGURES
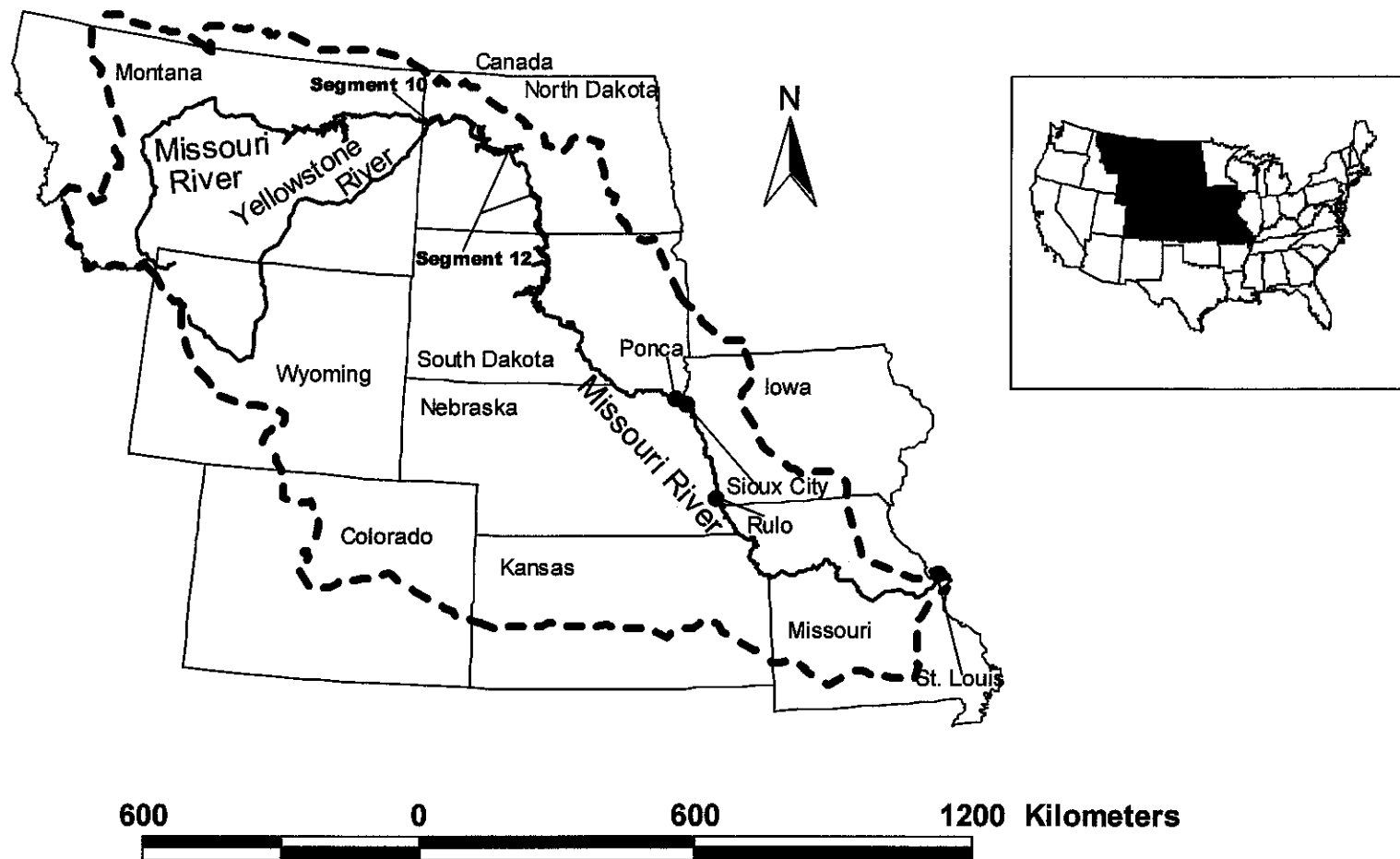
Figure 1.1. The Missouri River basin (thick broken line).
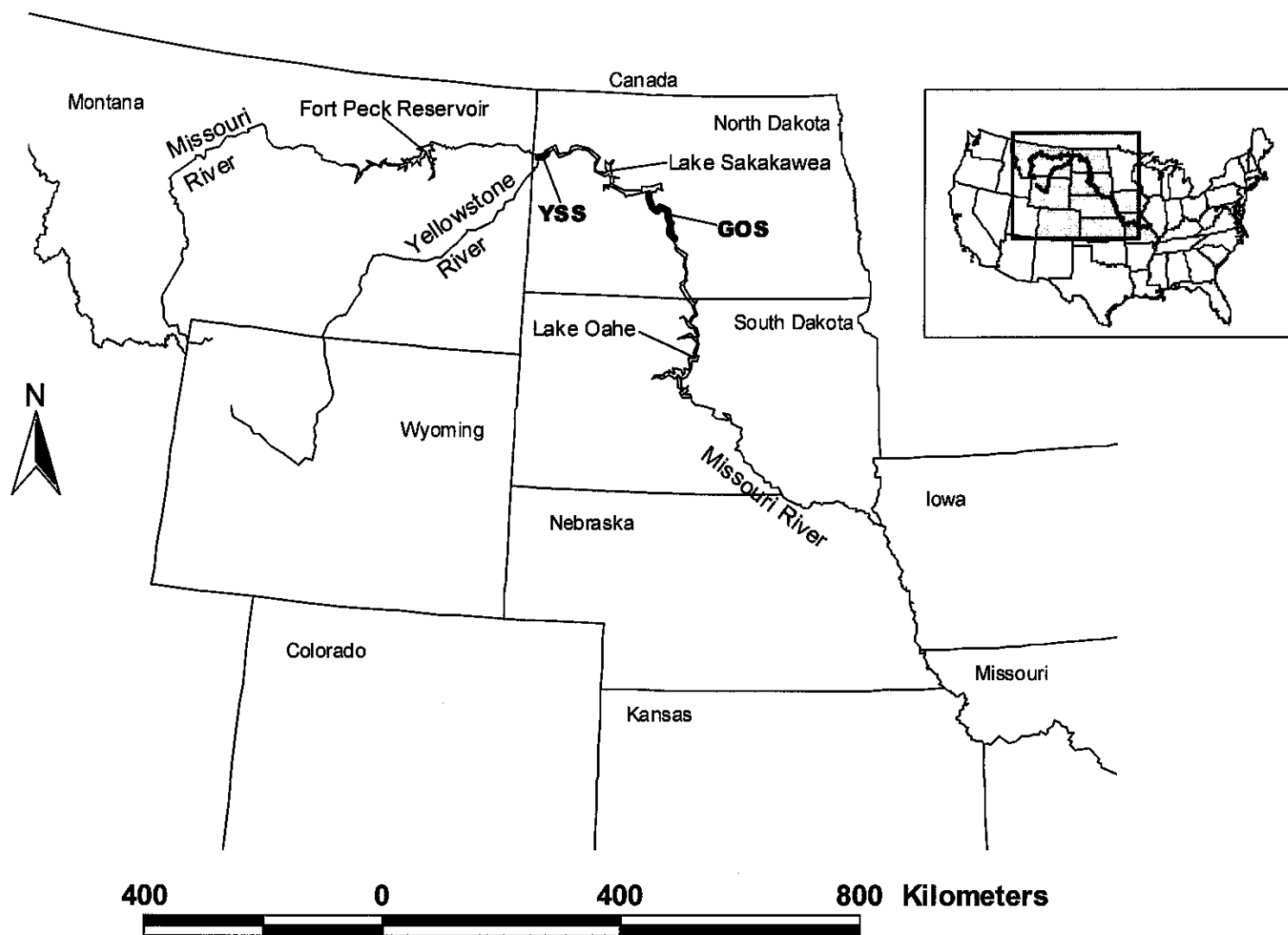
Figure 2.1. Map depicting study segments and location within Missouri River basin (GOS=Garrison-Oahe segment, YSS=Yellowstone-Sakakawea segment).

Figure 2.2. Location of macrohabitats in a typical Missouri River segment.

Outside Bend

Secondary Channel: Non-Connected

Main Channel Cross-Over

Inside Bend

Thalweg

Tributary Mouth

Secondary Channel: Connected
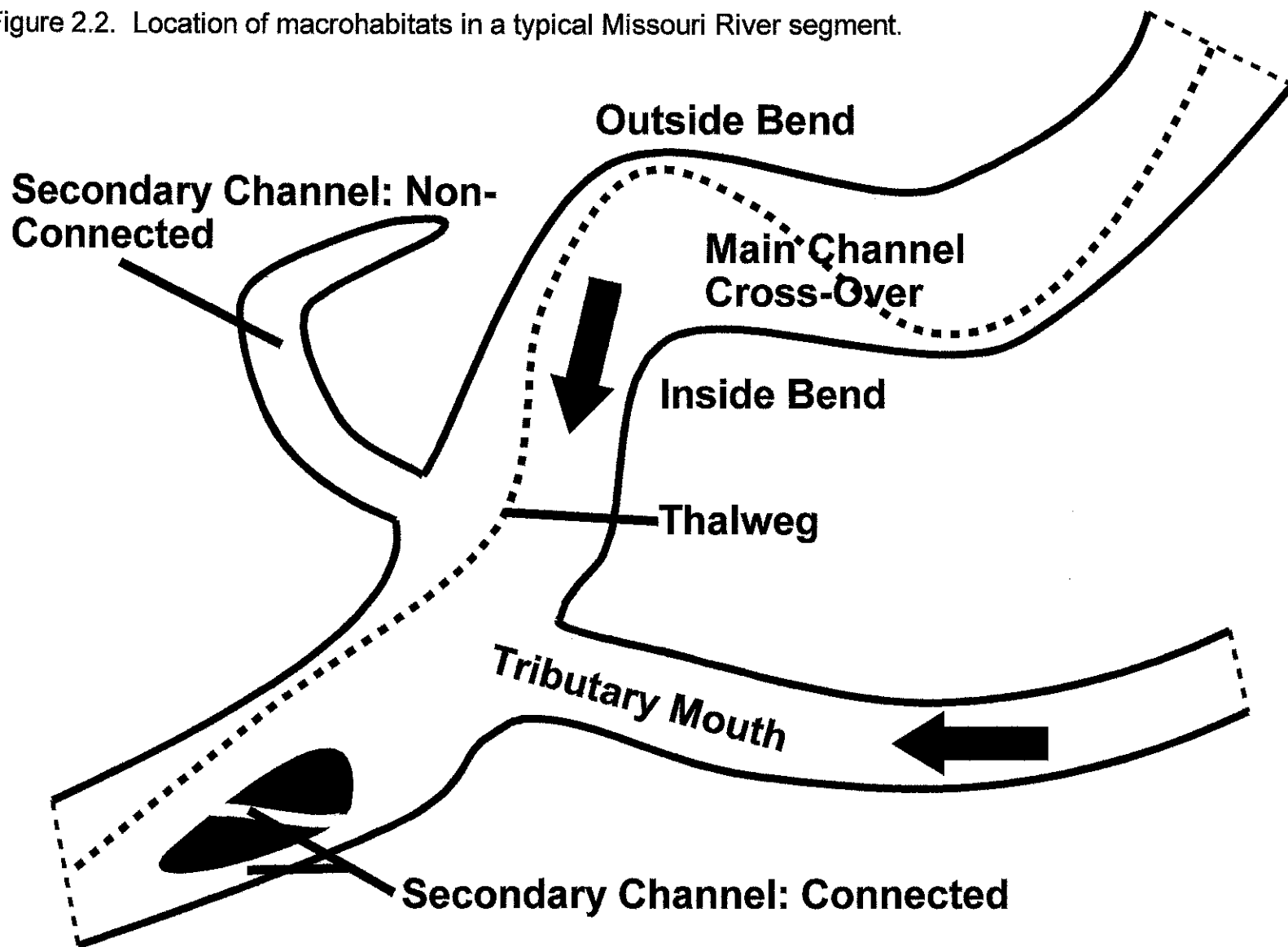
Figure 2.3. Explanatory diagram for interpretation of feeding strategy, niche width contribution, and prey importance (modified Costello method, Amundsen et al. 1996). BPC=between phenotype component to niche width, WPC=within phenotype component to niche width.
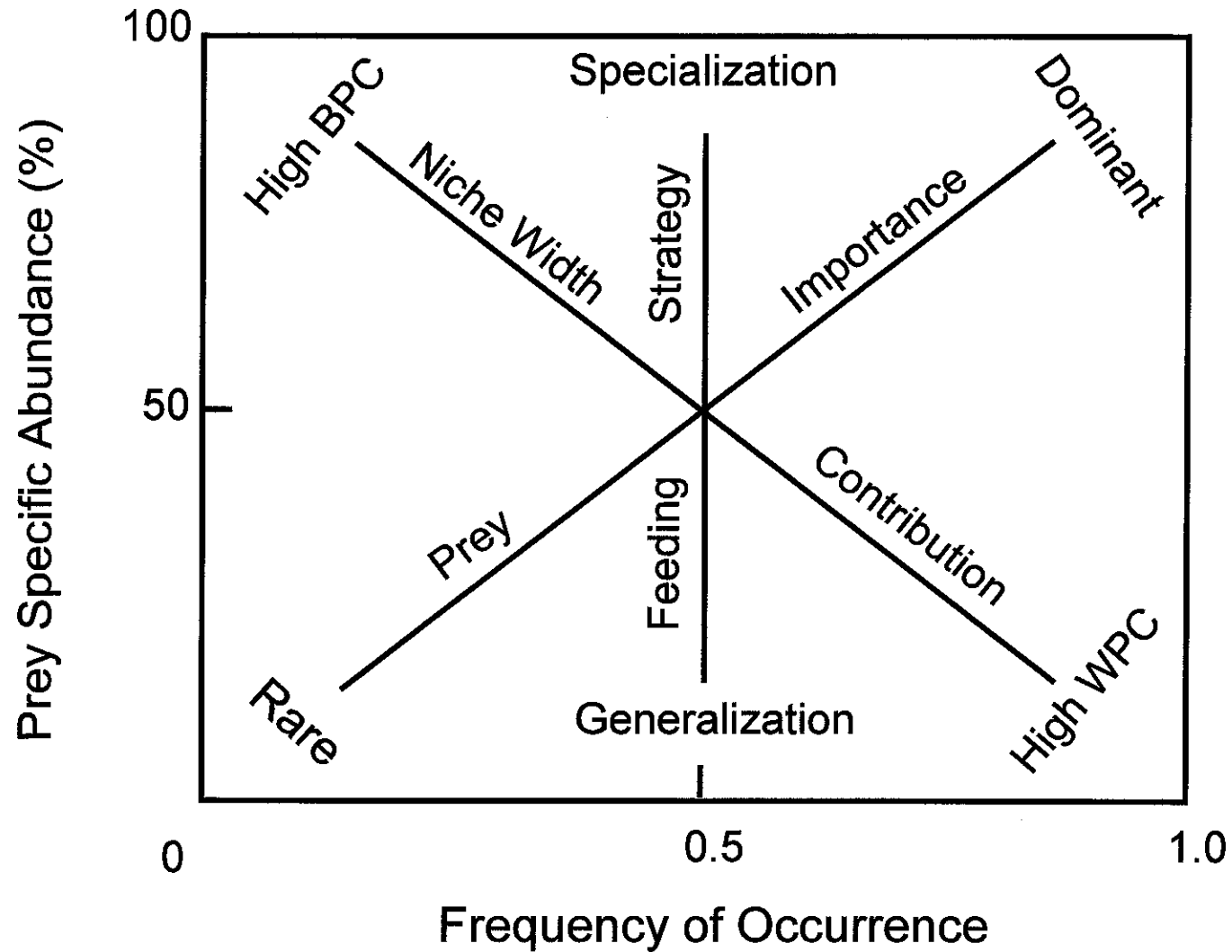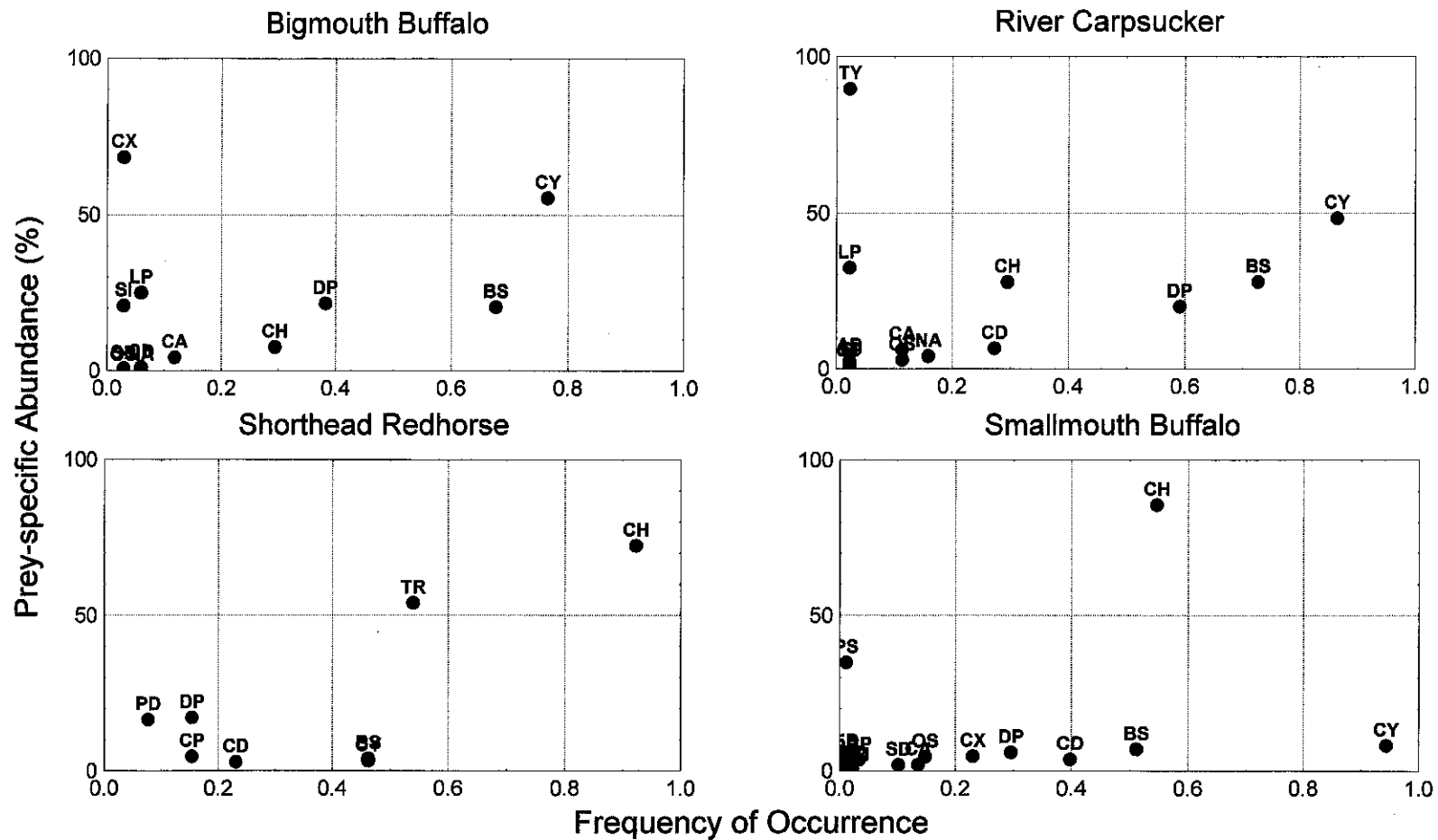
Figure 2.4. Graphs depicting feeding strategy and prey importance for YSS Catostomid species (for explanation of prey code, consult Tables 2.1-2.6).
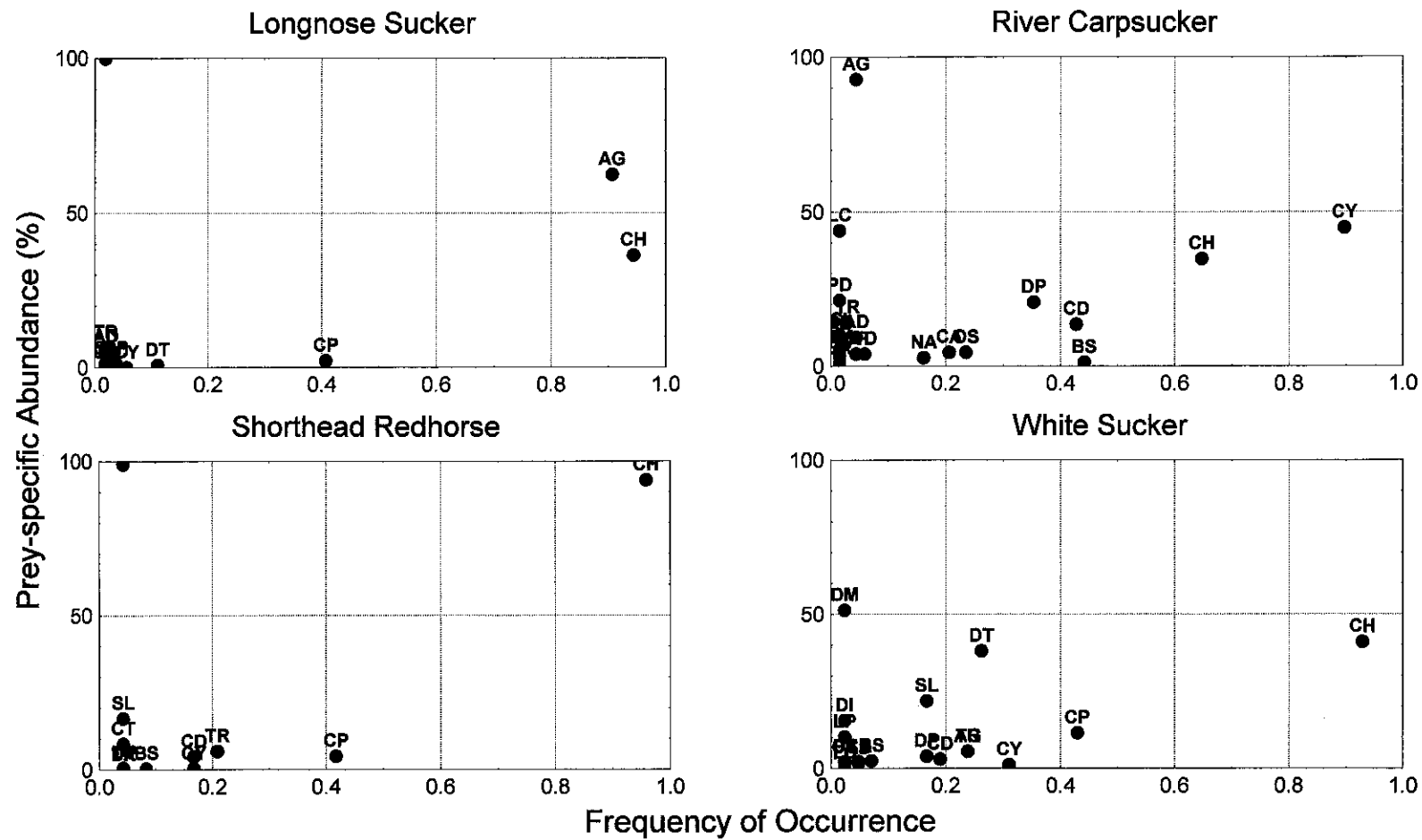
Figure 2.5. Graphs depicting feeding strategy and prey importance for GOS Catostomid species (for explanation of prey code, consult Tables 2.1-2.6).
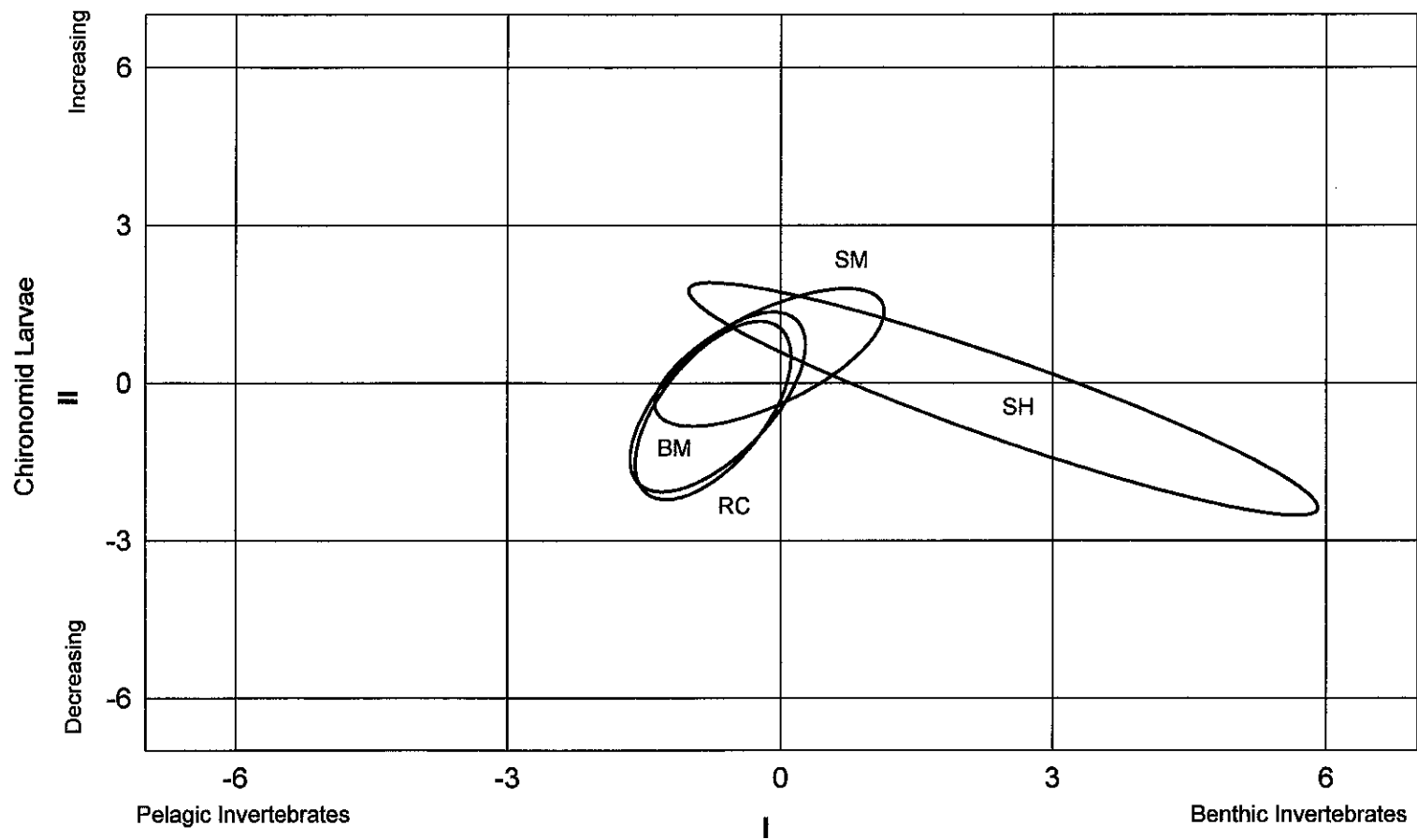
Figure 2.6. Ellipses enclosing 70% of the individuals of each YSS Catostomid species plotted on canonical variables I (I) and II (II) (BM=bigmouth buffalo, RC=river carpsucker, SH=shorthead redhorse, SM=smallmouth buffalo).
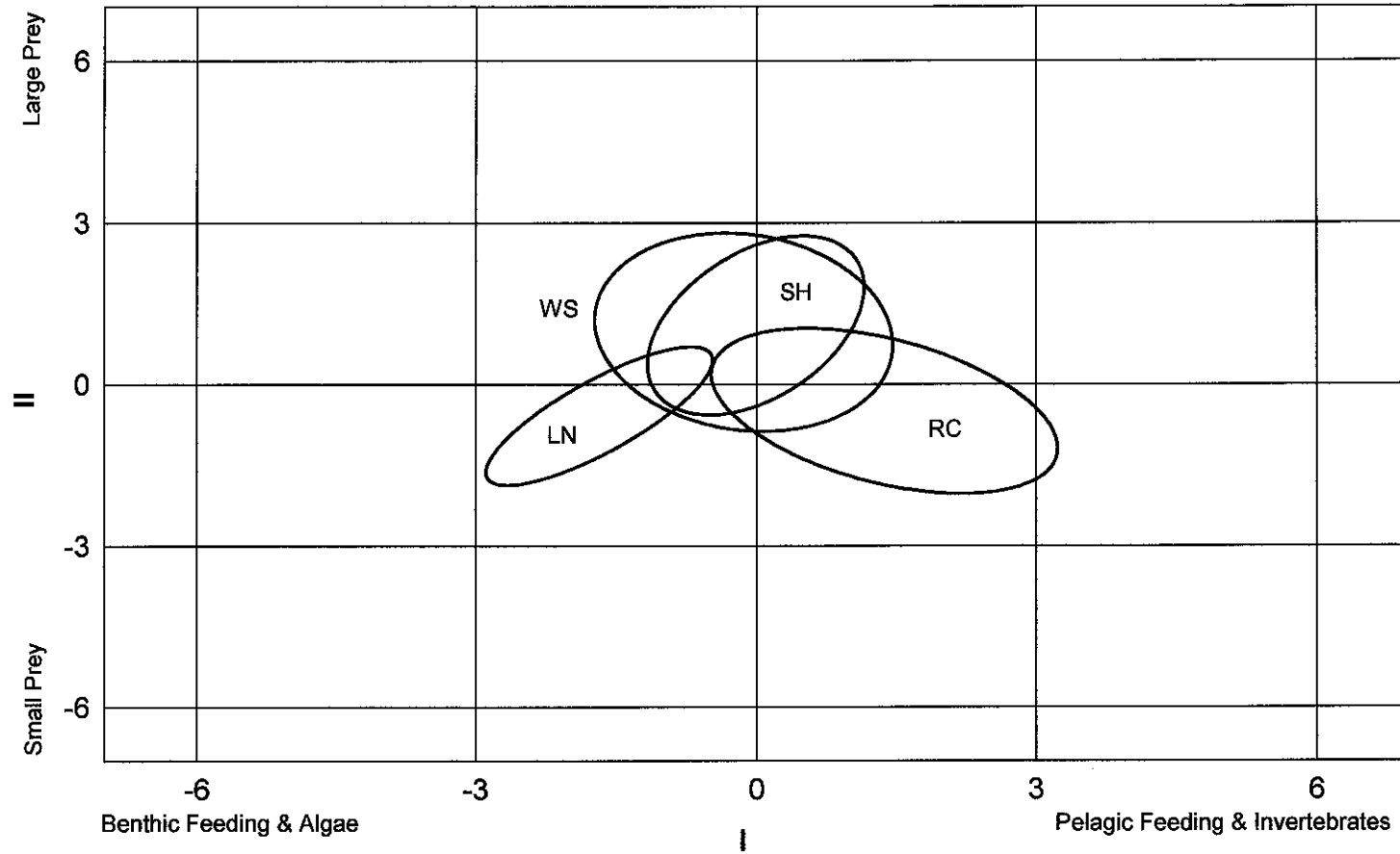
Figure 2.7. Ellipses enclosing 70% of the individuals of each GOS Catostomid species plotted on canonical variables I (I) and II (II) (LN=longnose sucker, RC=river carpsucker, SH=shorthead redhorse, WS=white sucker).
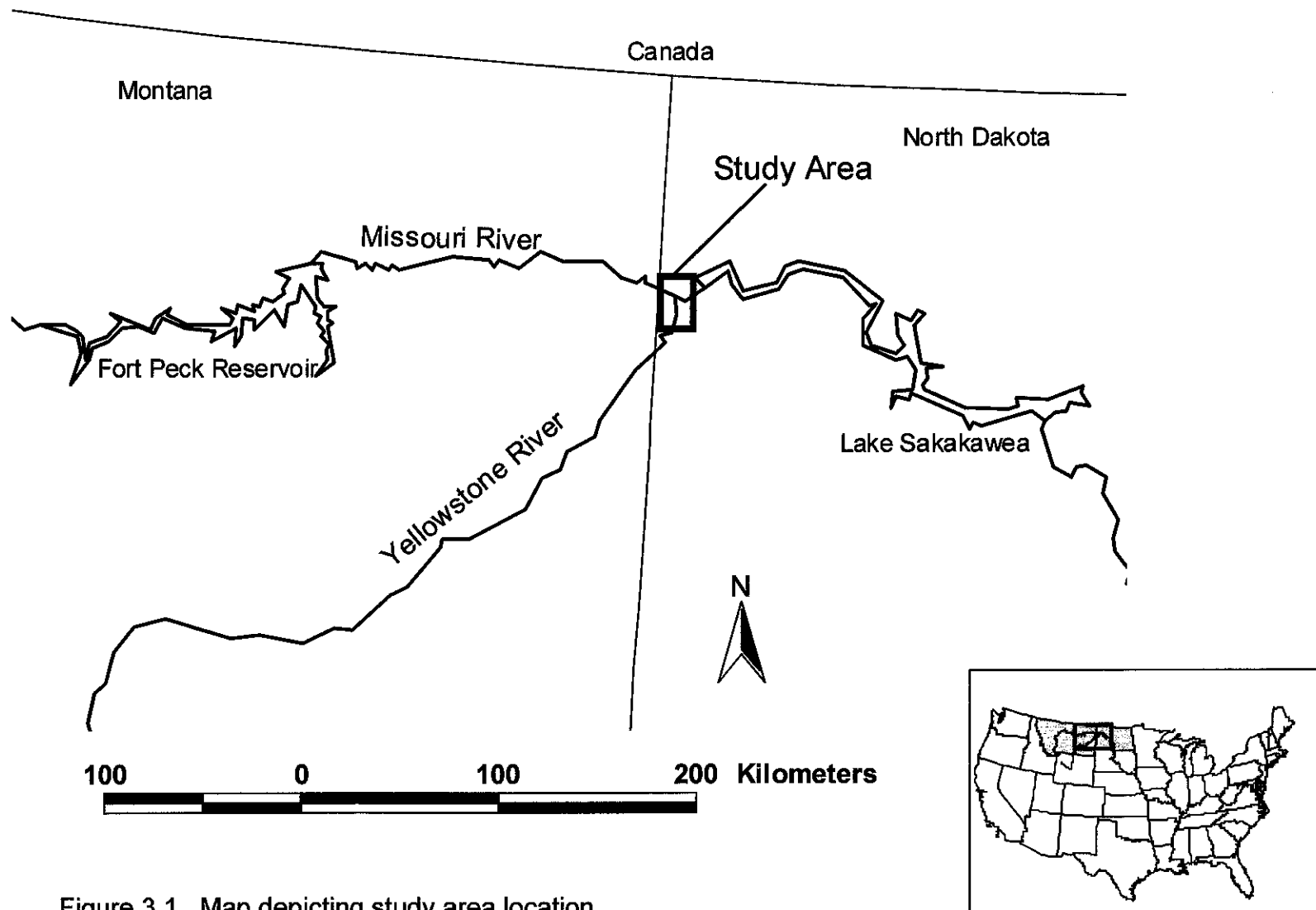
Figure 3.1. Map depicting study area location.
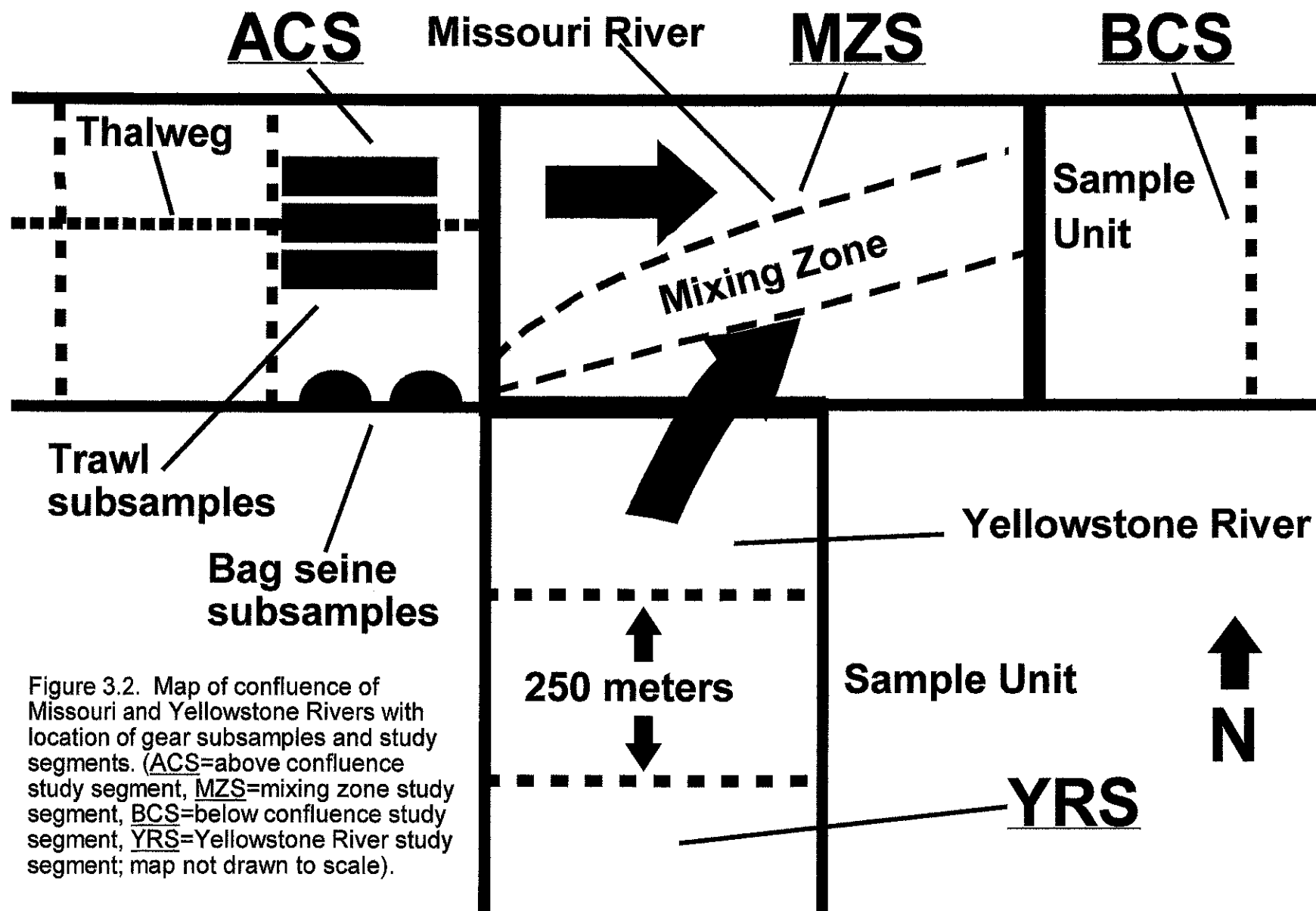
Figure 3.2. Map of confluence of Missouri and Yellowstone Rivers with location of gear subsamples and study segments. (ACS=above confluence study segment, MZS=mixing zone study segment, BCS=below confluence study segment, YRS=Yellowstone River study segment; map not drawn to scale).
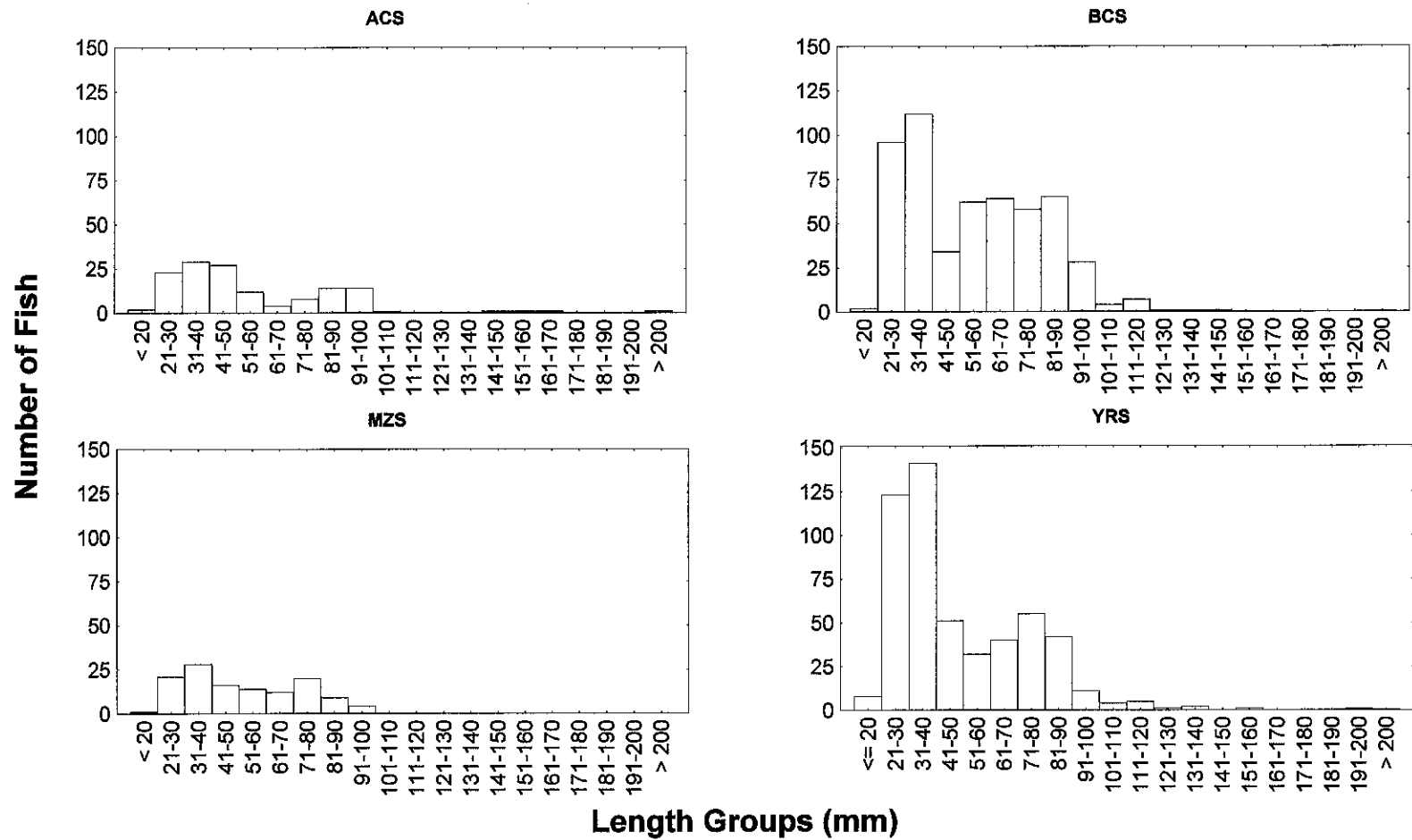
Figure 3.3. Length-frequency distributions for flathead chub by river segment (ACS=above confluence segment, BCS=below confluence segment, MZS=mixing zone segment, YRS=Yellowstone River segment).
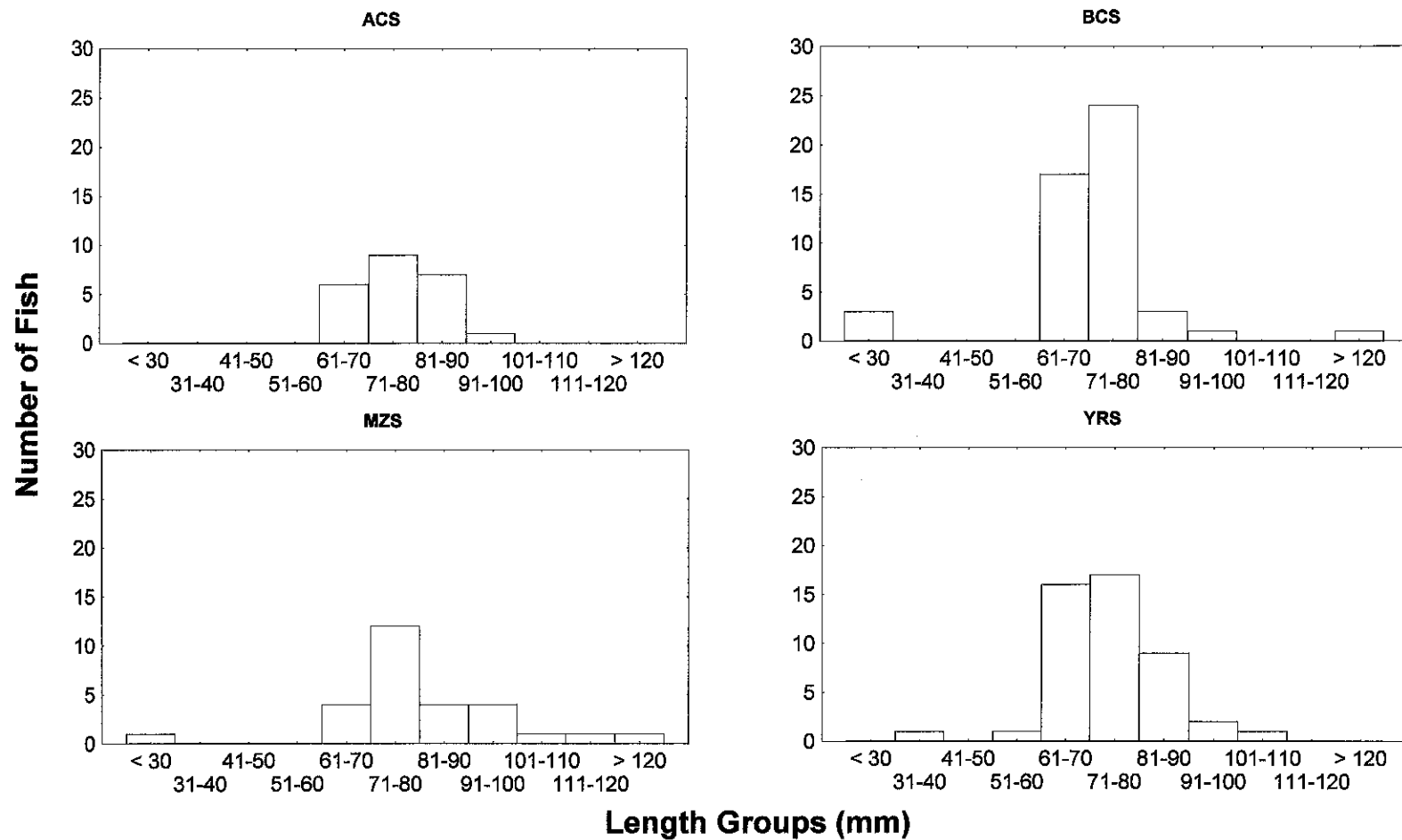
Figure 3.4. Length-frequency distributions for sicklefin chub by river segment (ACS=above confluence segment, BCS=below confluence segment, MZS=mixing zone segment, YRS=Yellowstone River segment).
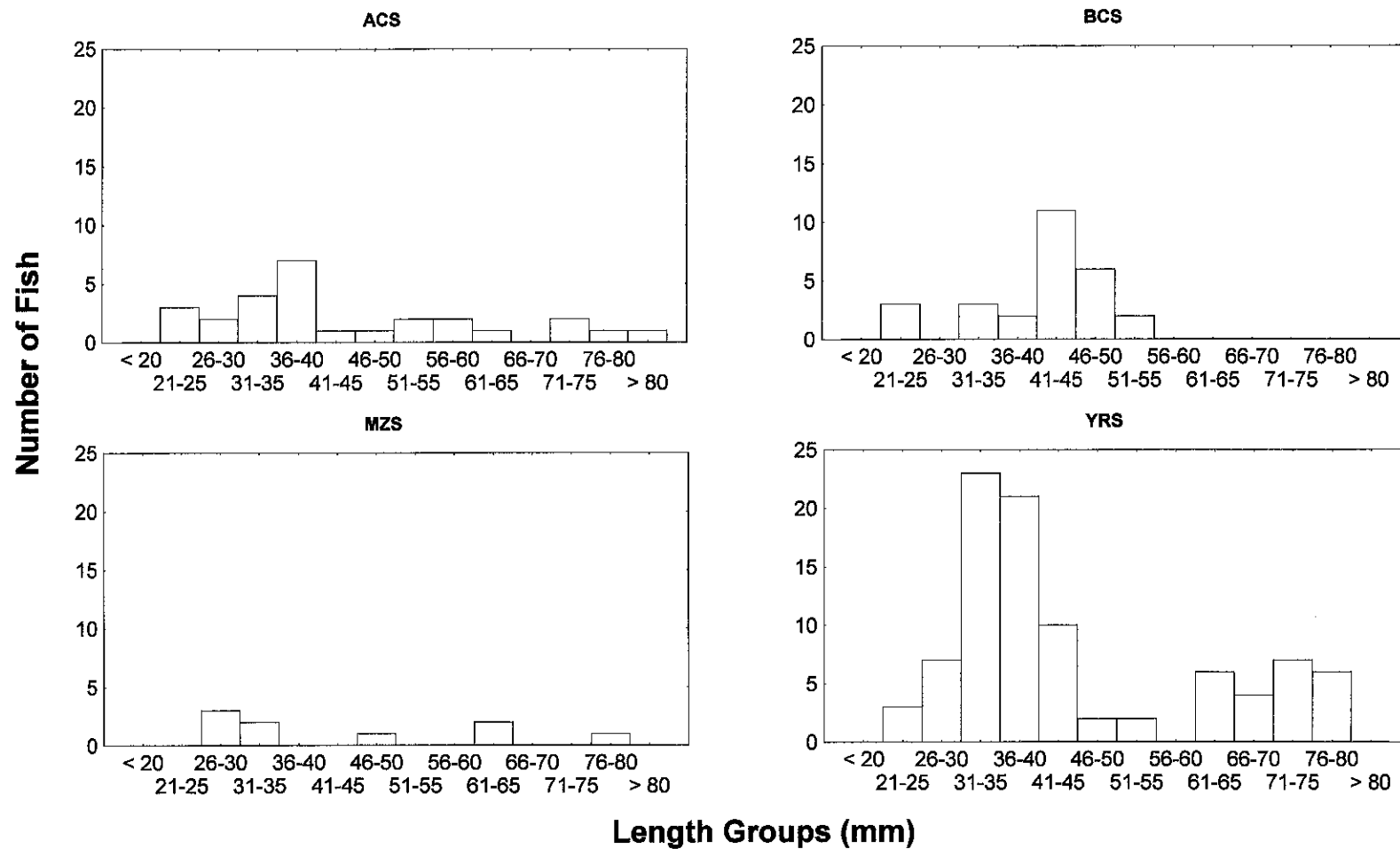
Figure 3.5. Length-frequency distributions for sturgeon chub by river segment (ACS=above confluence segment, BCS=below confluence segment, MZS=mixing zone segment, YRS=Yellowstone River segment).
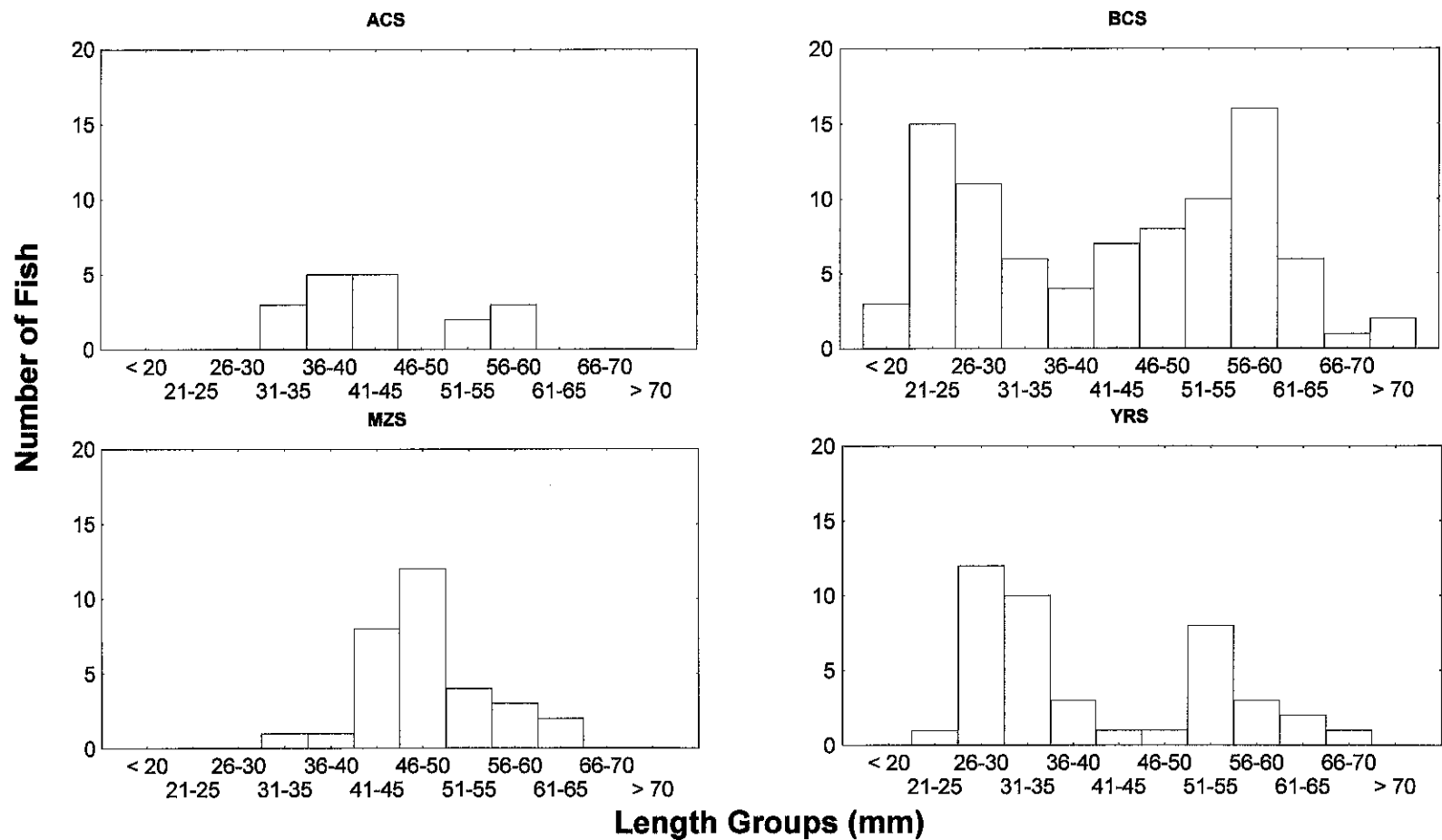
Figure 3.6. Length-frequency distributions for western silvery minnow by river segment (ACS=above confluence segment, BCS=below confluence segment, MZS=mixing zone segment, YRS=Yellowstone River segment).
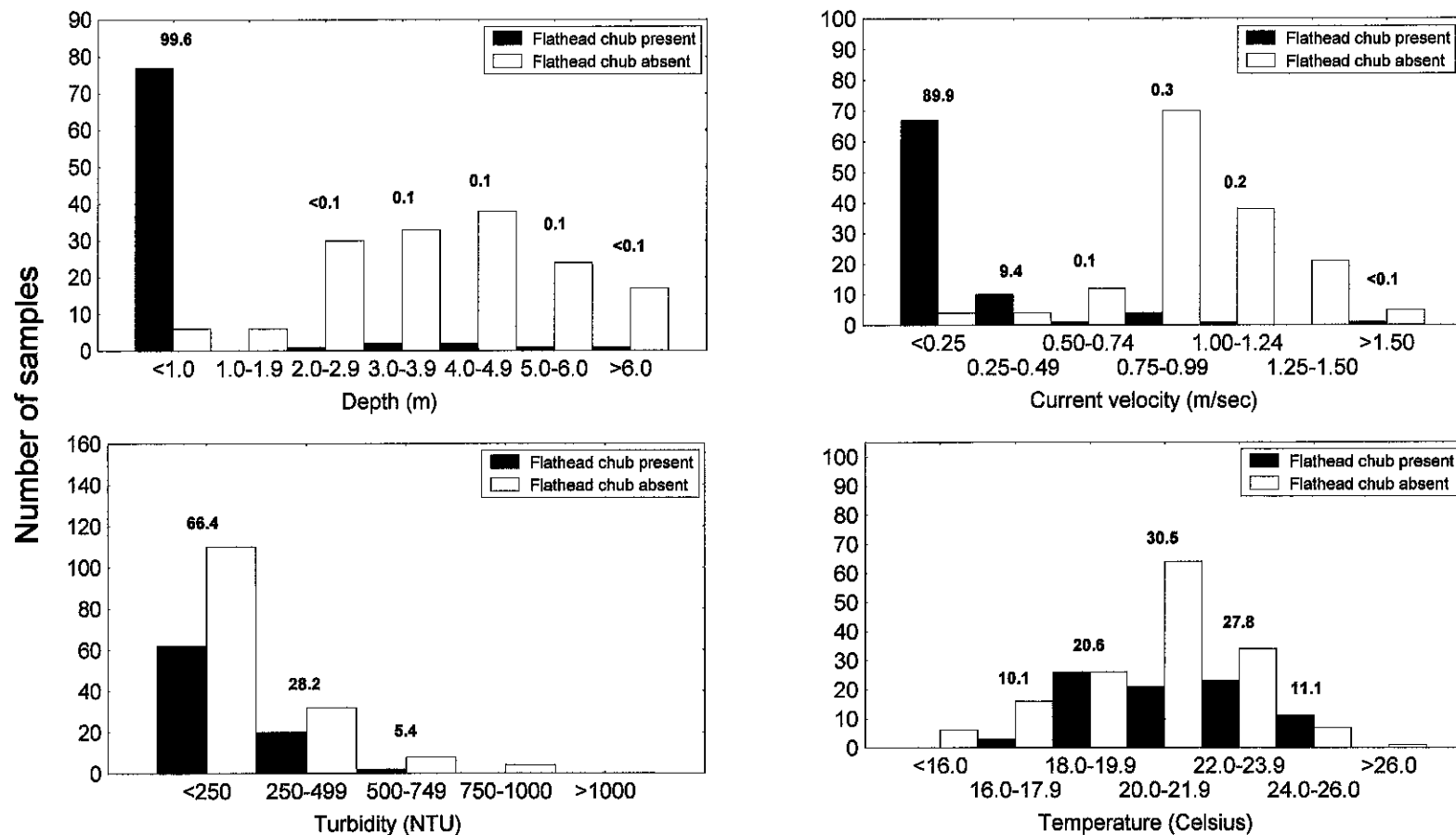
Figure 3.7. Characterization of habitat where flathead chub where captured. A sample represents a single bag seine haul or benthic trawl tow. Numbers above bars represent the percentage of fish captured in that category.
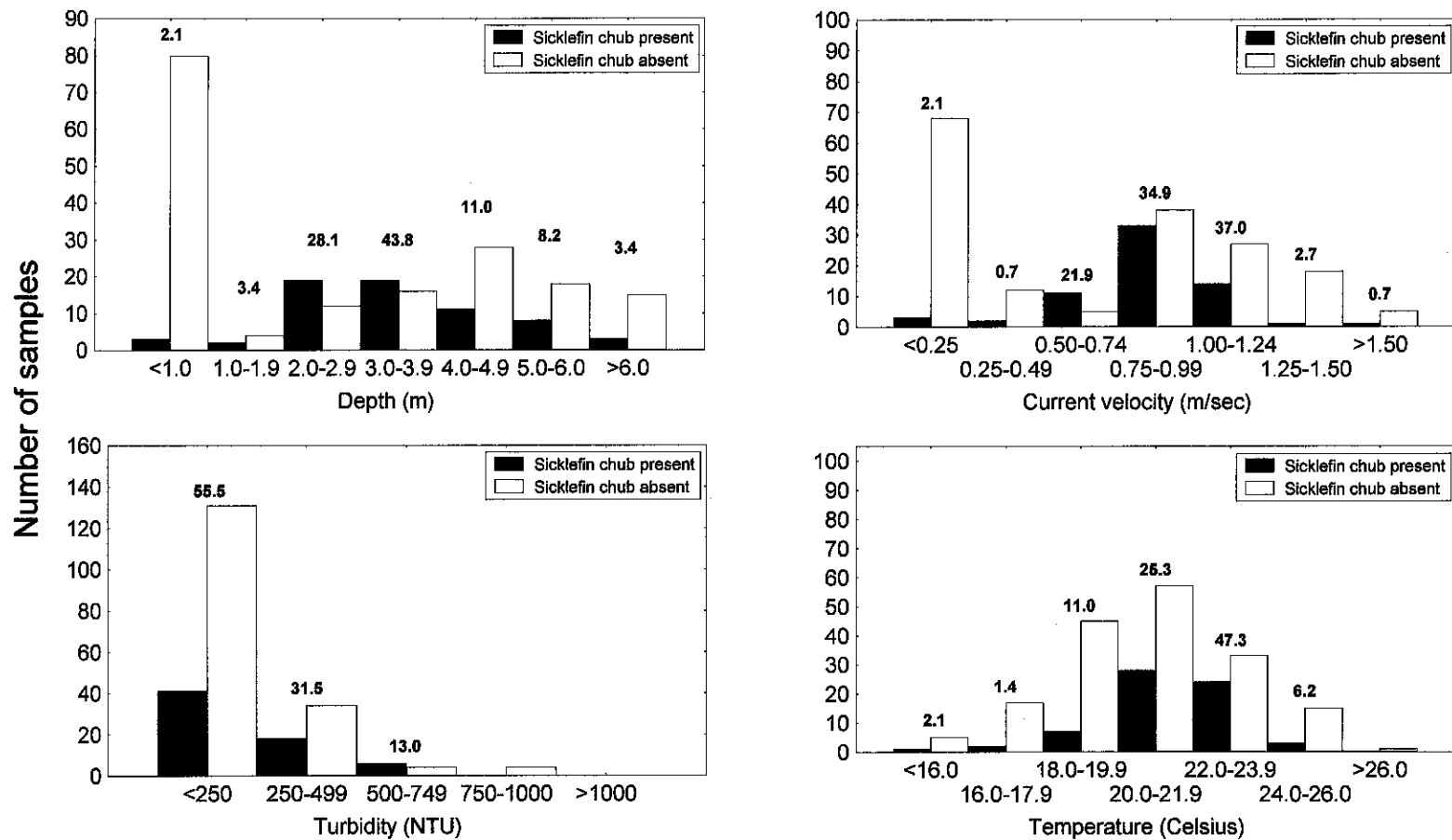
Figure 3.8. Characterization of habitat where sicklefin chub where captured. A sample represents a single bag seine haul or benthic trawl tow. Numbers above bars represent the percentage of fish captured in that category.
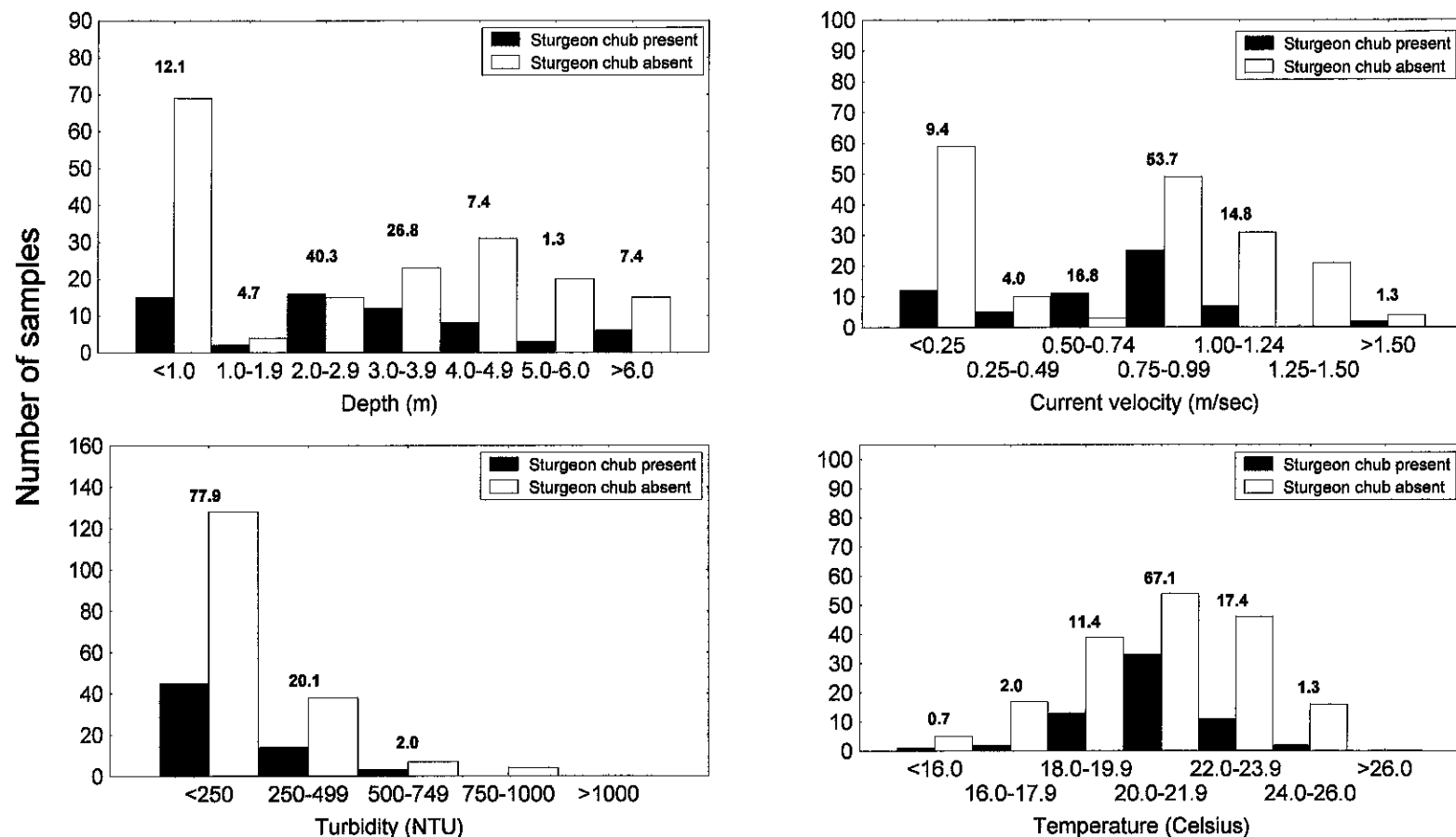
Figure 3.9. Characterization of habitat where sturgeon chub were captured. A sample represents a single bag seine haul or benthic trawl tow. Numbers above bars represent the percentage of fish captured in that category.
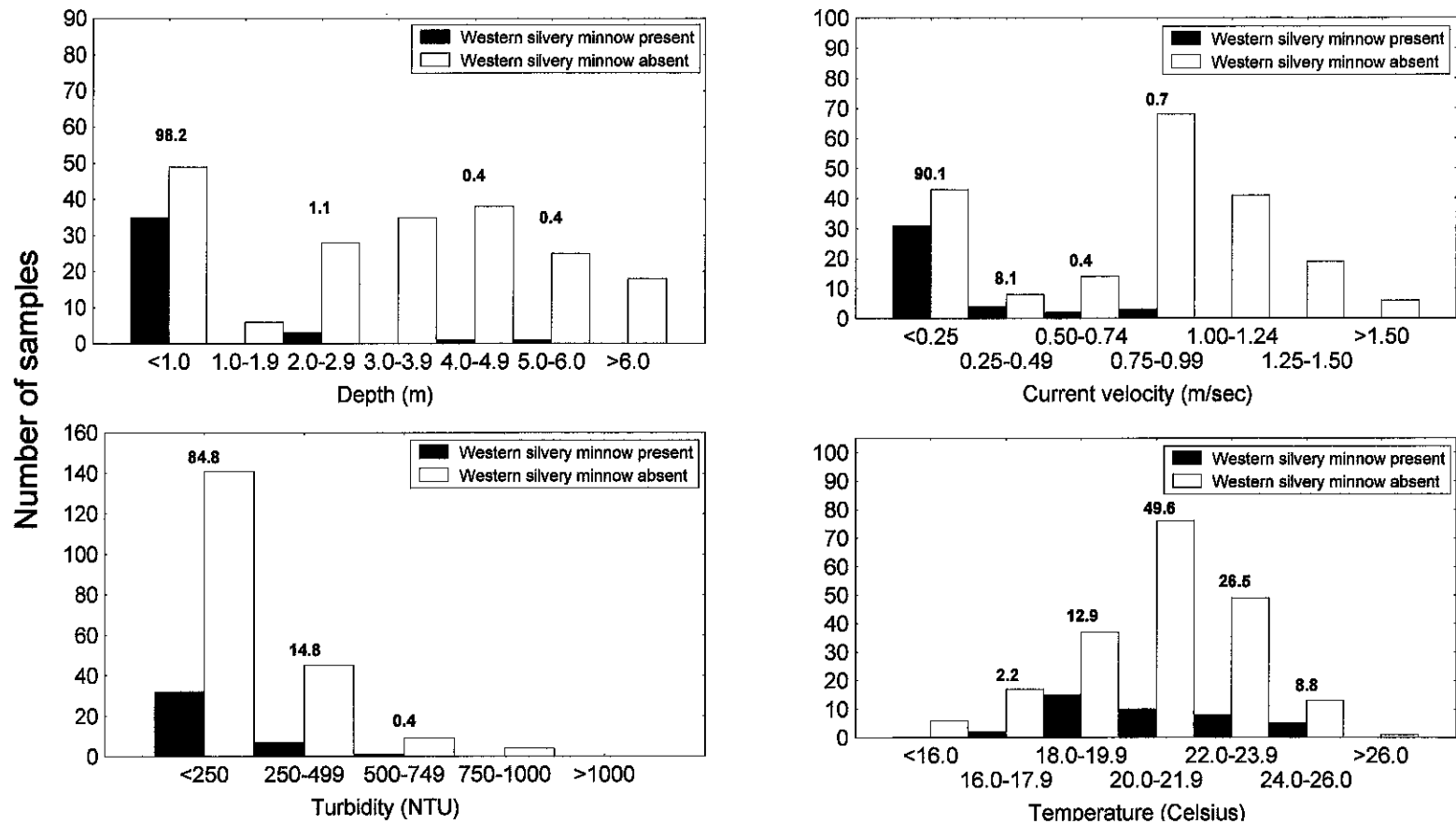
Figure 3.10. Characterization of habitat where western silvery minnow were captured. A sample represents a single bag seine haul or benthic trawl tow. Numbers above bars represent the percentage of fish captured in that category.
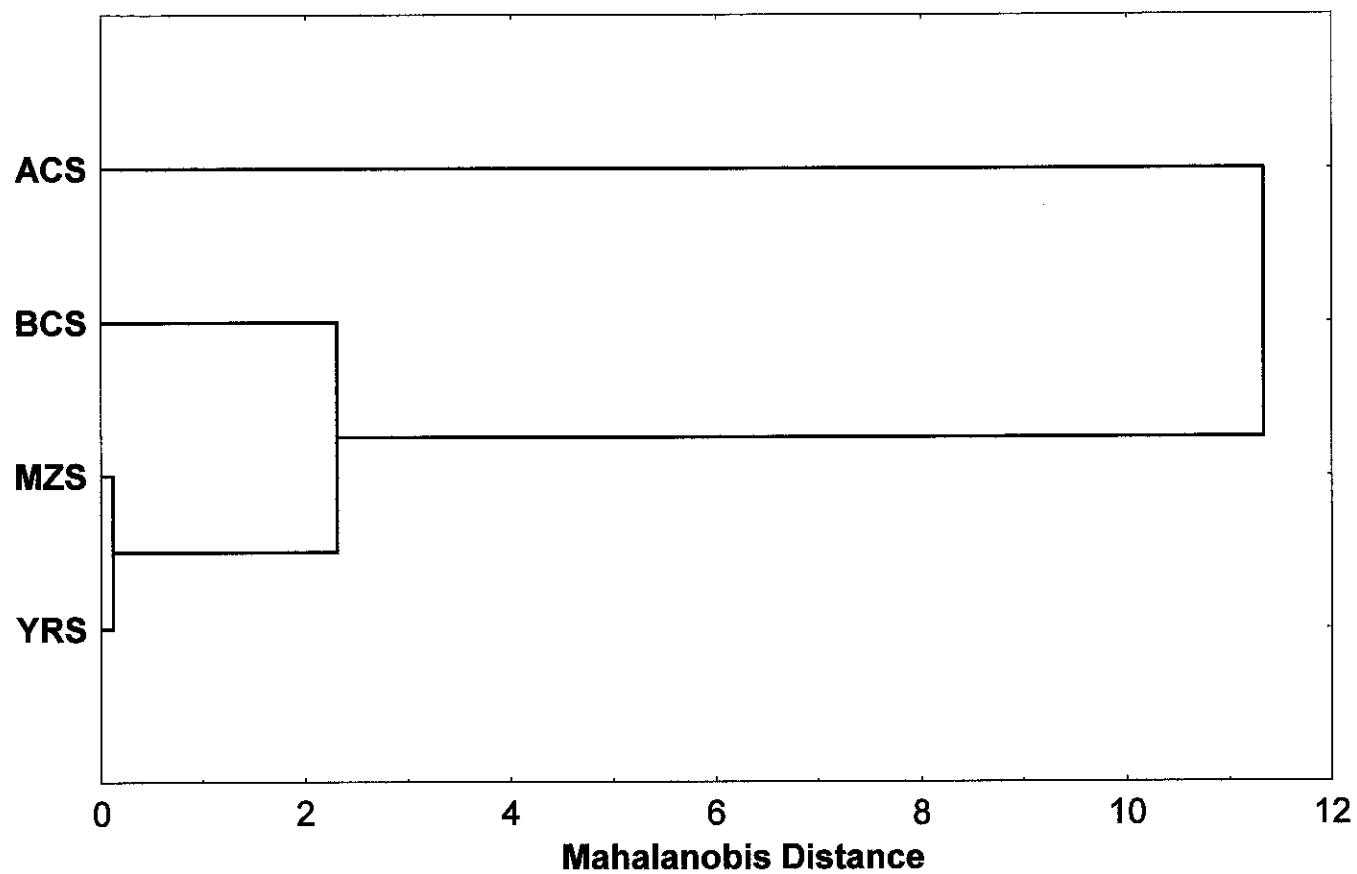
Figure 3.11. Cluster analysis of physiochemical data collected from the four study segments. (AC=above confluence segment, BC=below confluence segment, MZ=mixing zone, YS=Yellowstone River segment).
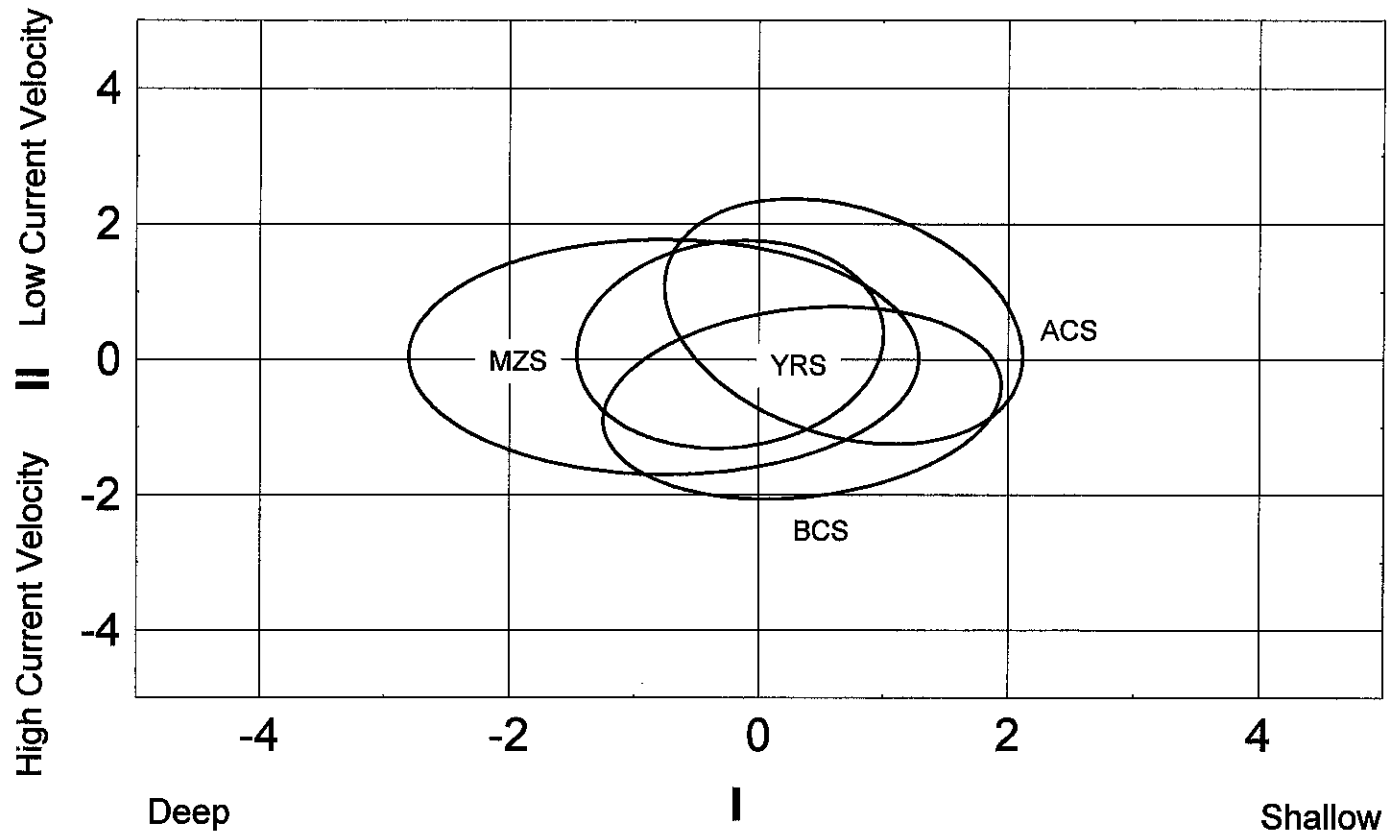
Figure 3.12. Ellipses enclosing 70% of cases of each study segment plotted on canonical variables I (I) and II (II). Canonical variables derived from physiochemical data collected from main channel habitat. (ACS=above confluence segment, BCS=below confluence segment, MZS=mixing zone segment, YRS=Yellowstone River segment).
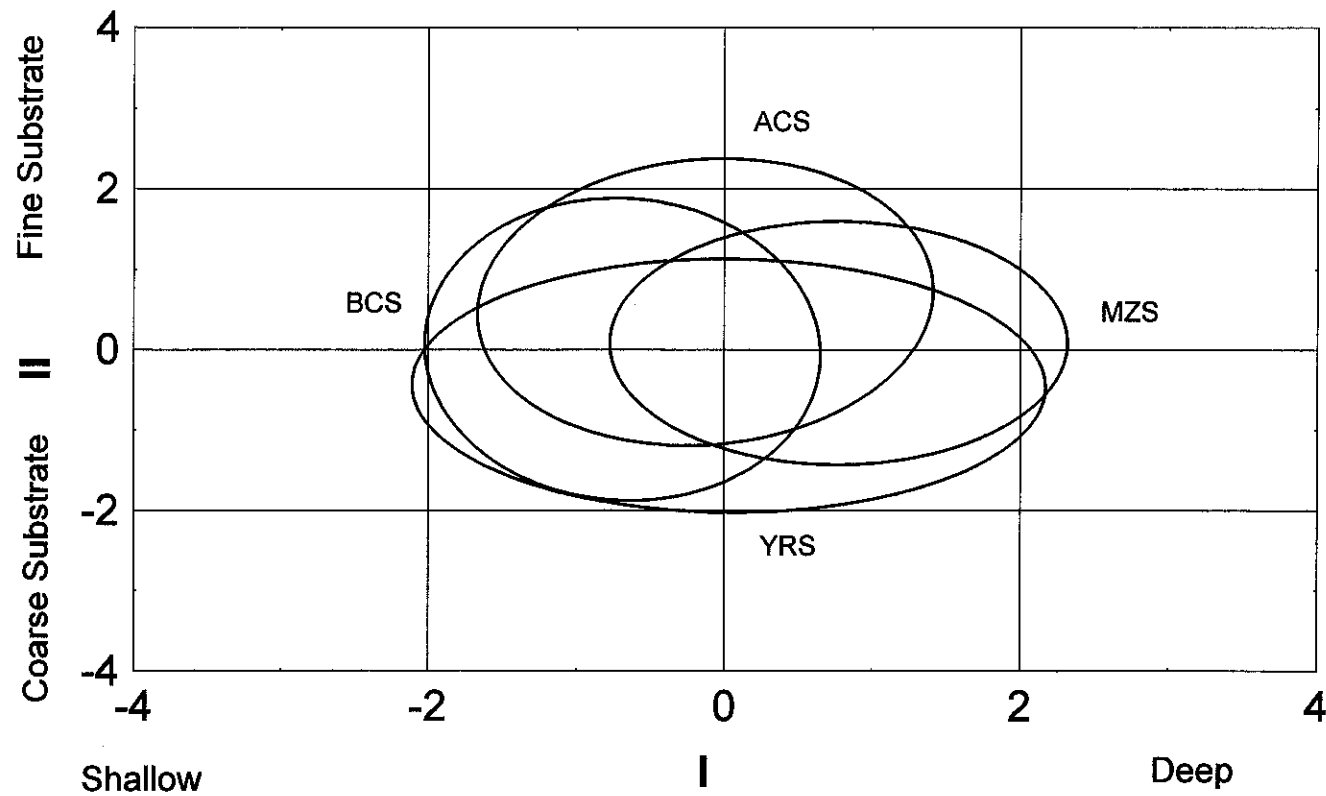
Figure 3.13. Ellipses enclosing 70% of cases of each study segment plotted on canonical variables I (I) and II (II). Canonical variables derived from physiochemical data collected from channel border habitat. (ACS=above confluence segment, BCS=below confluence segment, MZS=mixing zone segment, YRS=Yellowstone River segment).
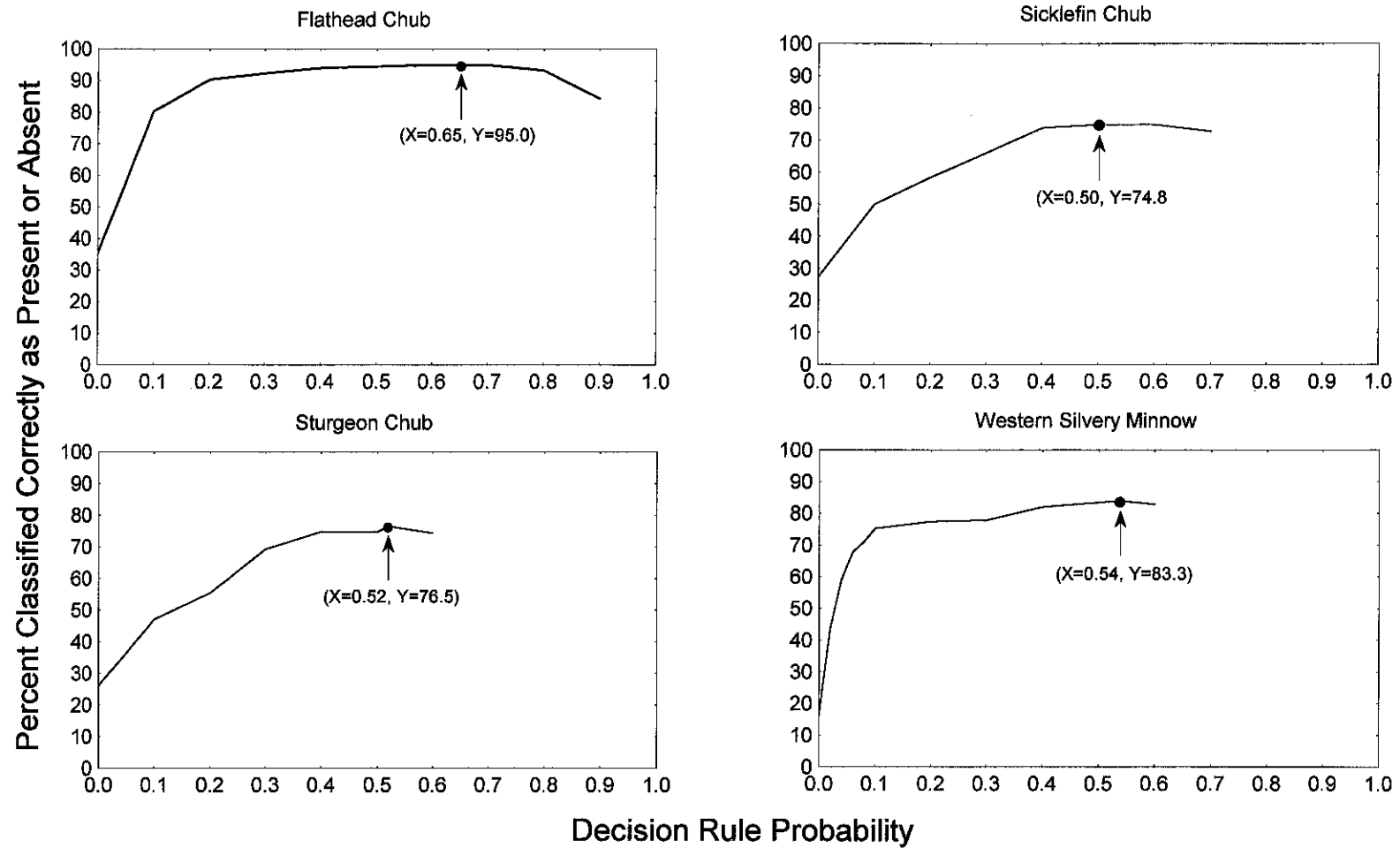
Figure 3.14. Graphs depicting relationship between percent of four cyprinid species correctly classified as present or absent and decision rule probability.
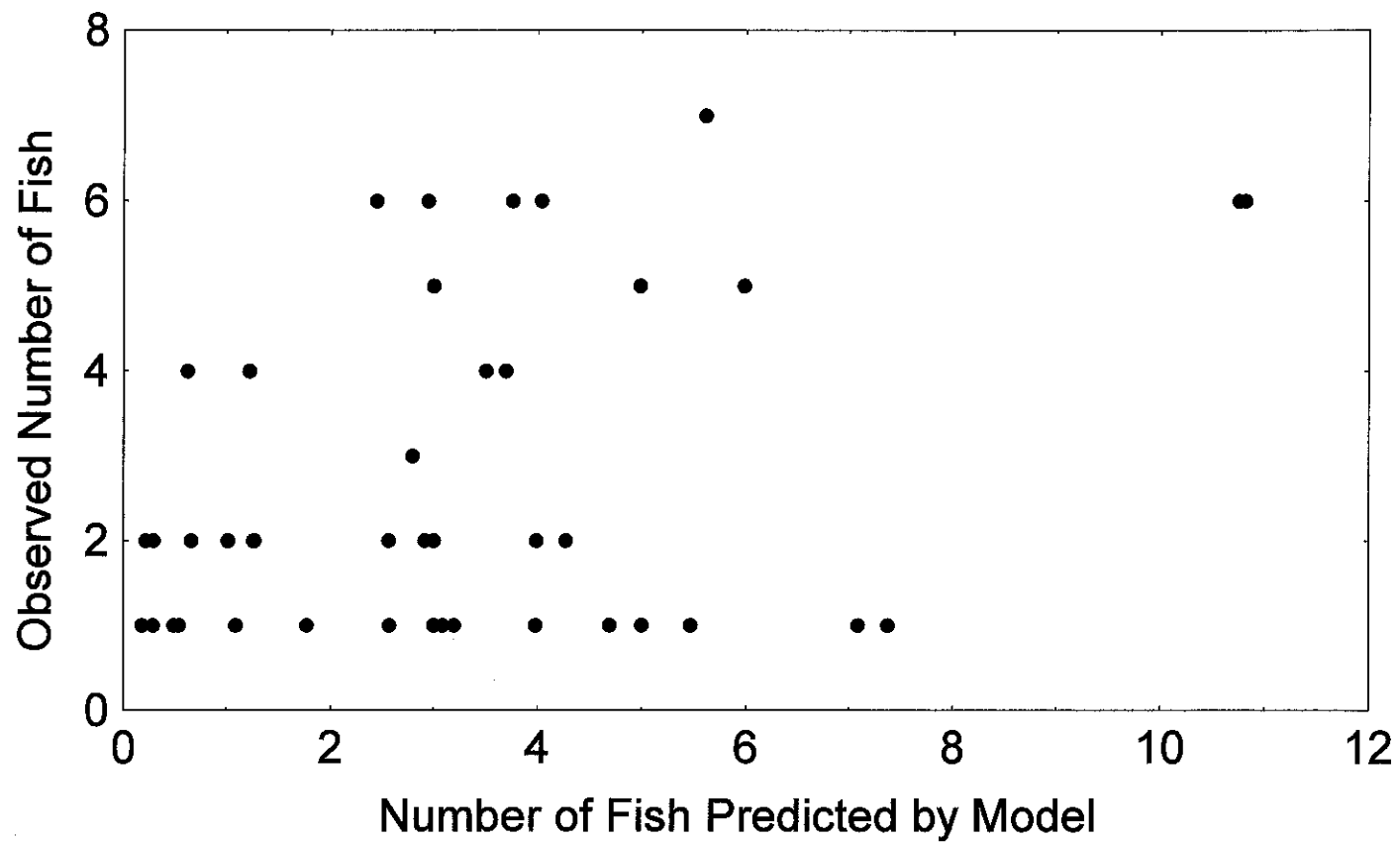
Figure 3.15. Relation between observed number of sicklefin chub and number of chubs predicted by Poisson regression model.
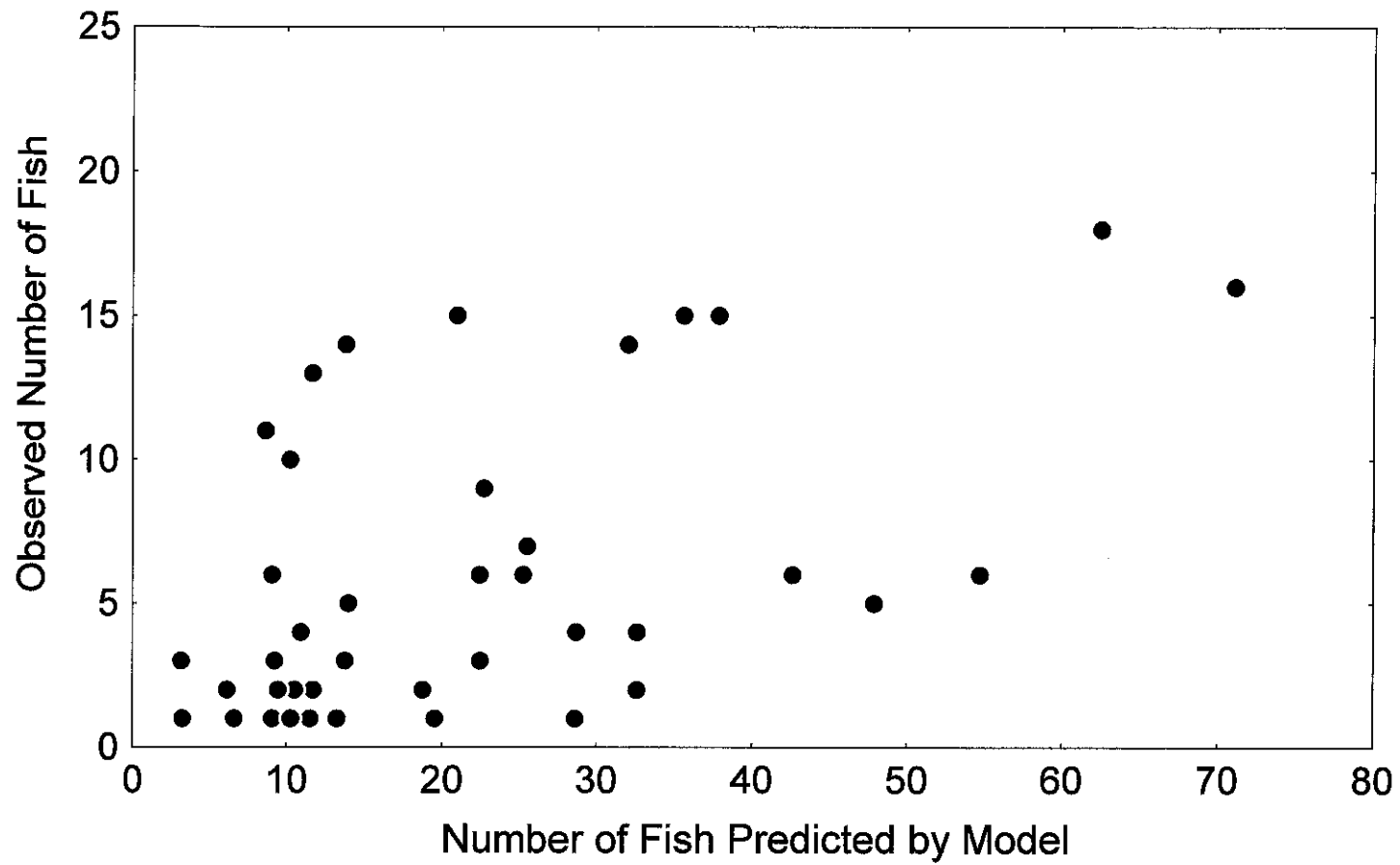
Figure 3.16. Relation between observed number of sturgeon chub and number of chubs predicted by Poisson regression model.
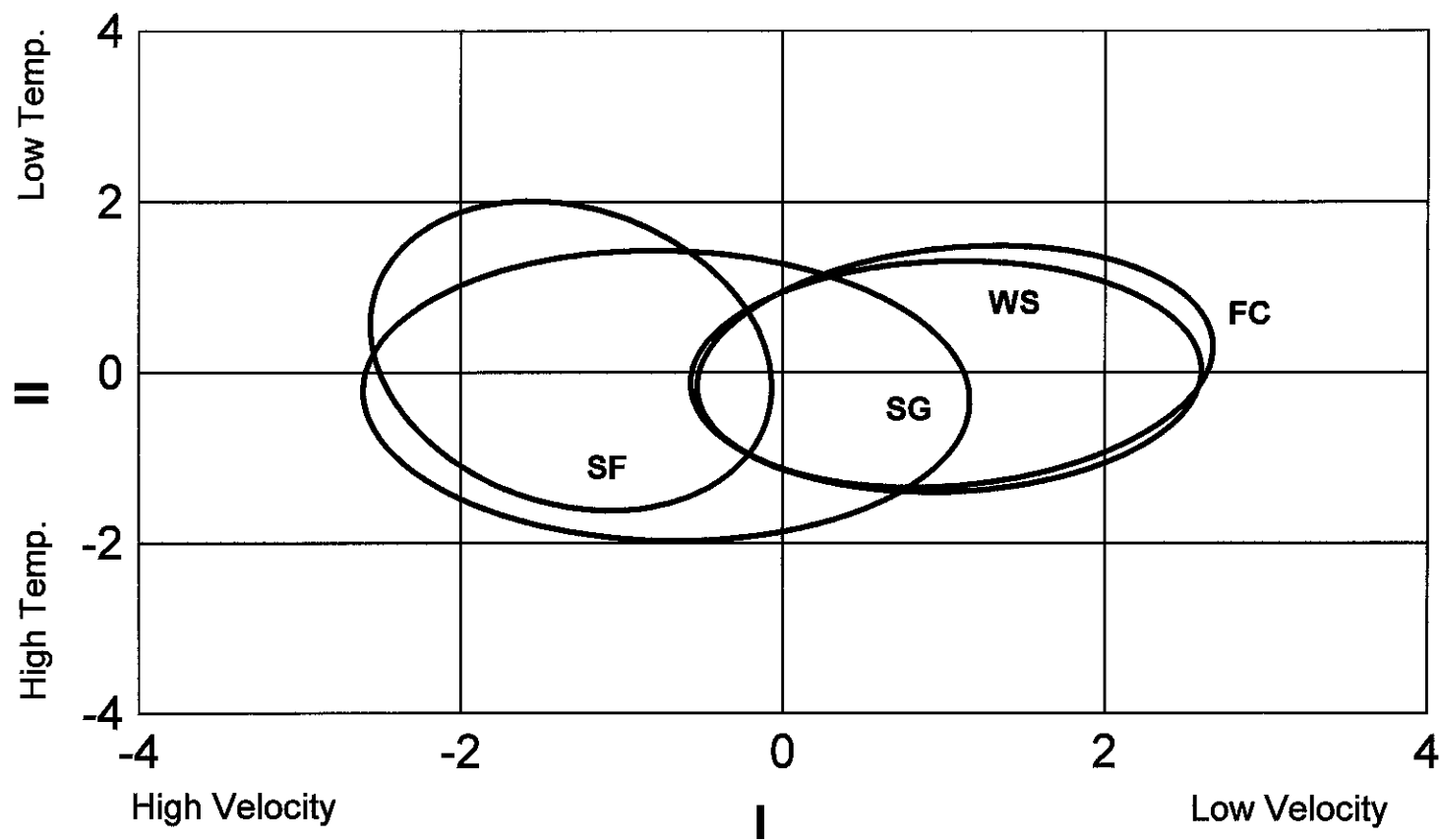
Figure 3.17. Ellipses enclosing 70% of individuals of each fish species plotted on canonical variables I (I) and II (II). (Temp.=Temperature; FC=flathead chub, SF=sicklefin chub, SG=sturgeon chub, WS=western silvery minnow).
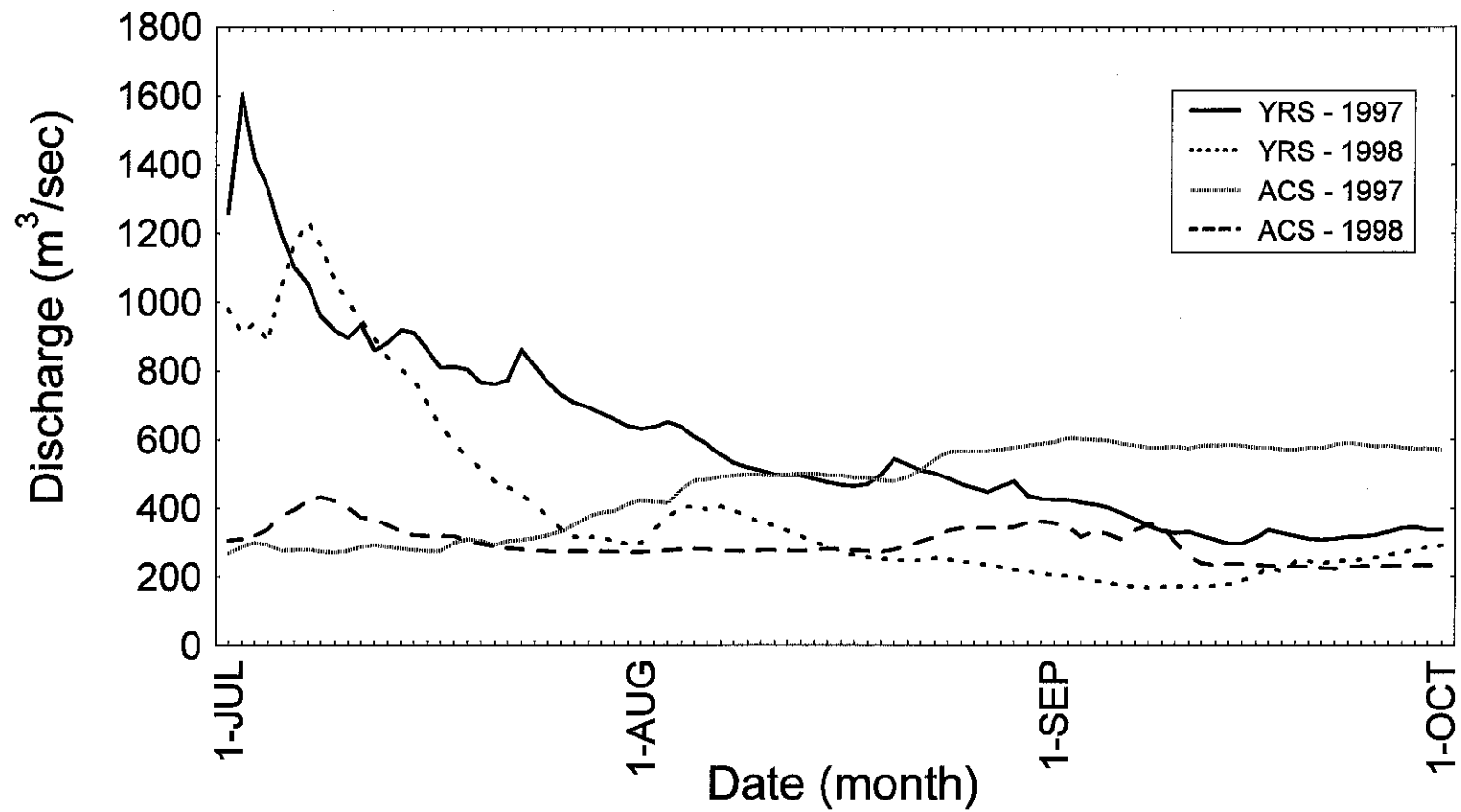
Figure 3.18. Mean daily discharge for the Yellowstone River segment (YRS; measured at Sidney, MT) and the above confluence segment (ACS; measured at Culbertson, MT) during study months in 1997 and 1998 (U. S. Geological Survey 1999).
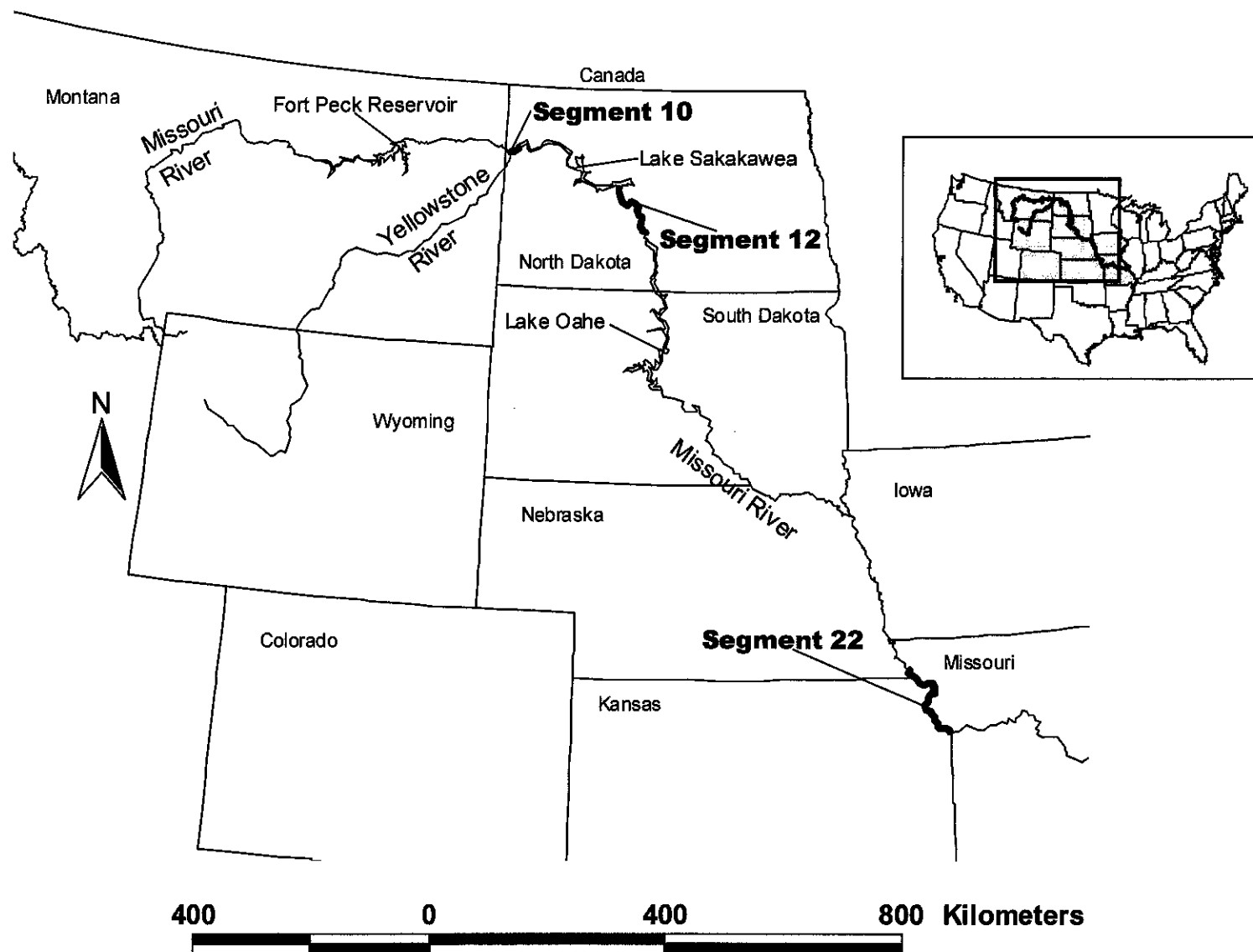
Figure 4.1. Map showing location of study segments

Figure 4.2. Location of macrohabitats in a typical Missouri River segment.

Outside Bend

Secondary Channel: Non-Connected

Main Channel Cross-Over

Inside Bend

Thalweg

Tributary Mouth

Secondary Channel: Connected
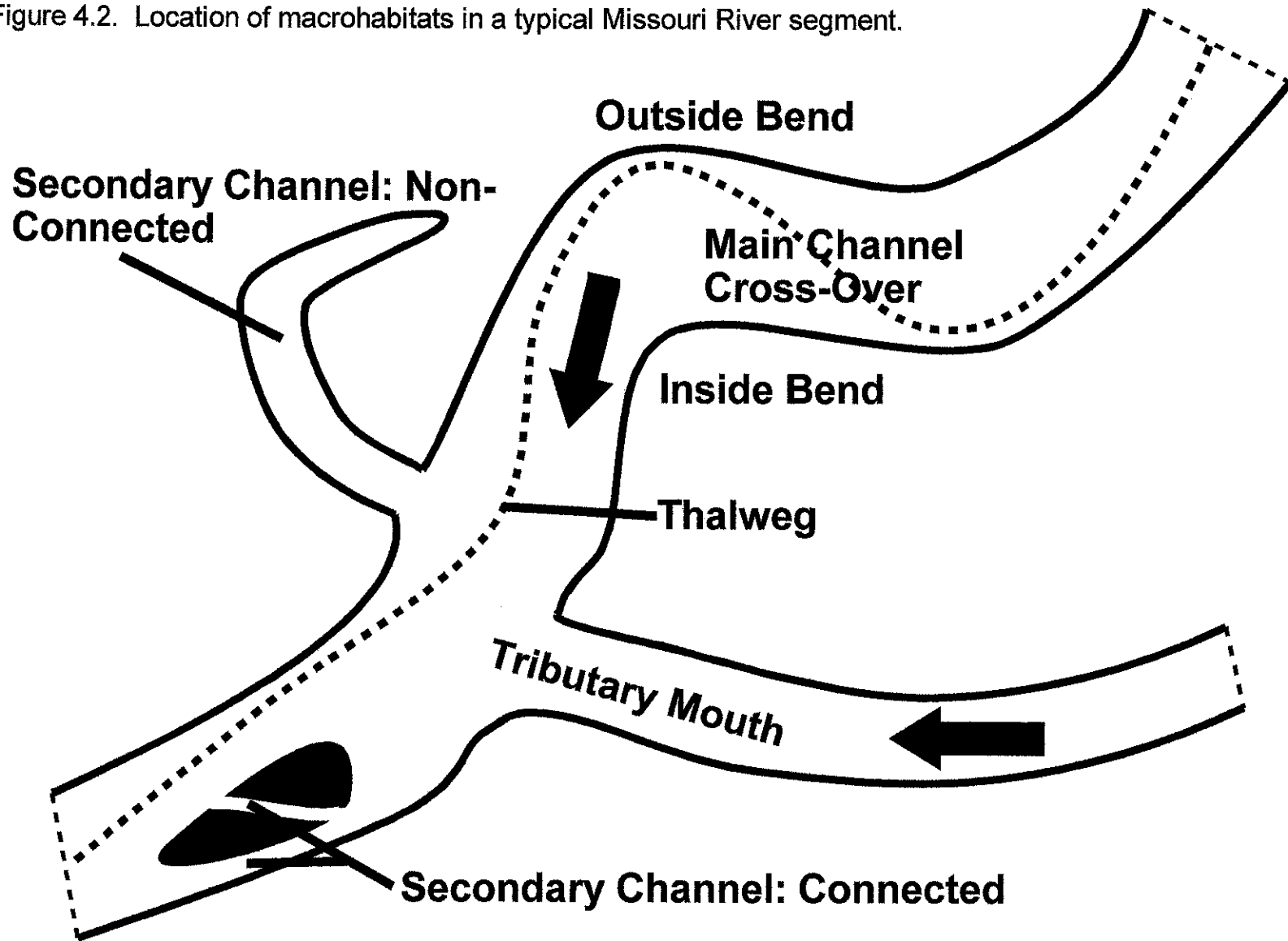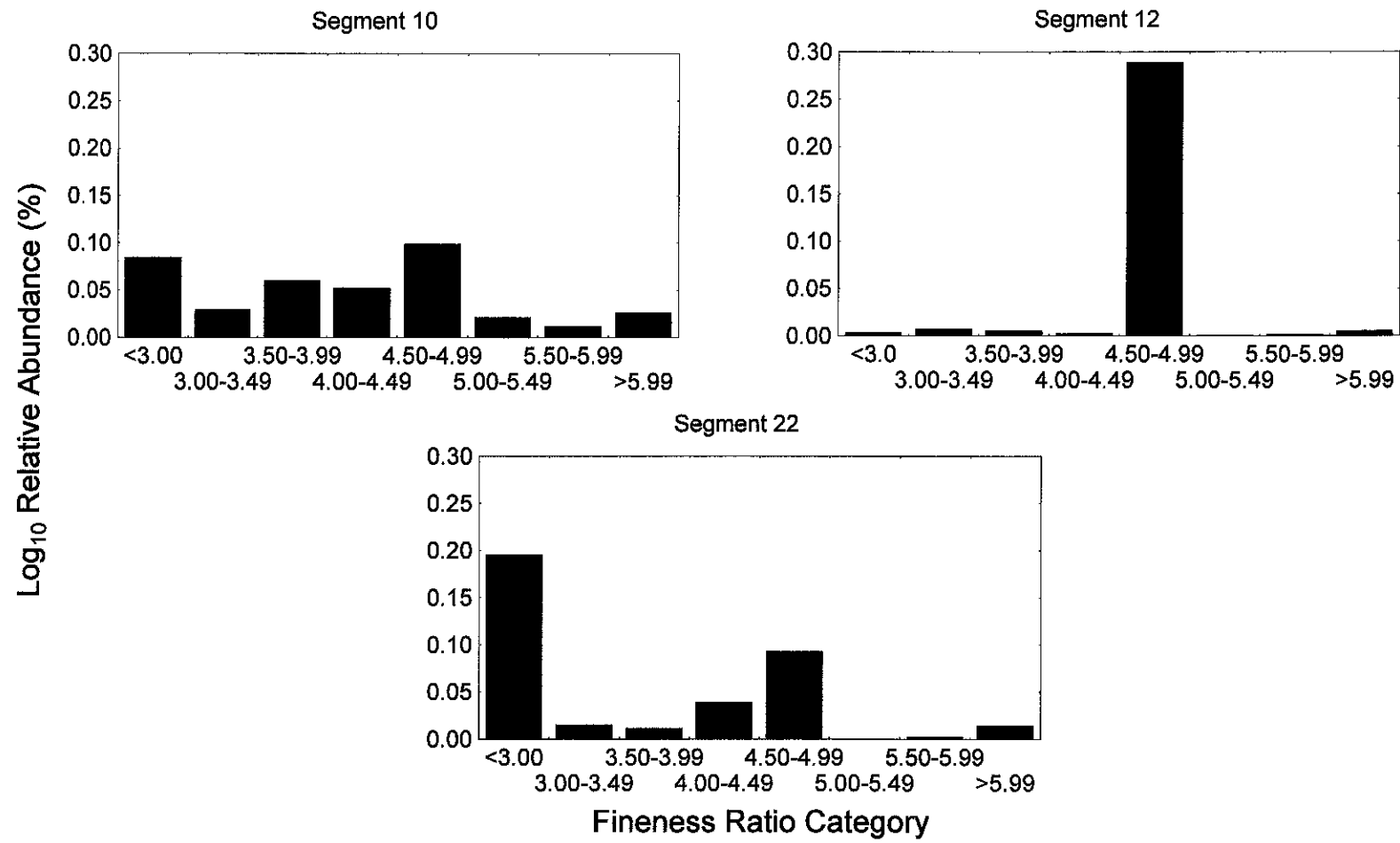
Figure 4.3. Relative abundance of fineness ratio categories in study segments.
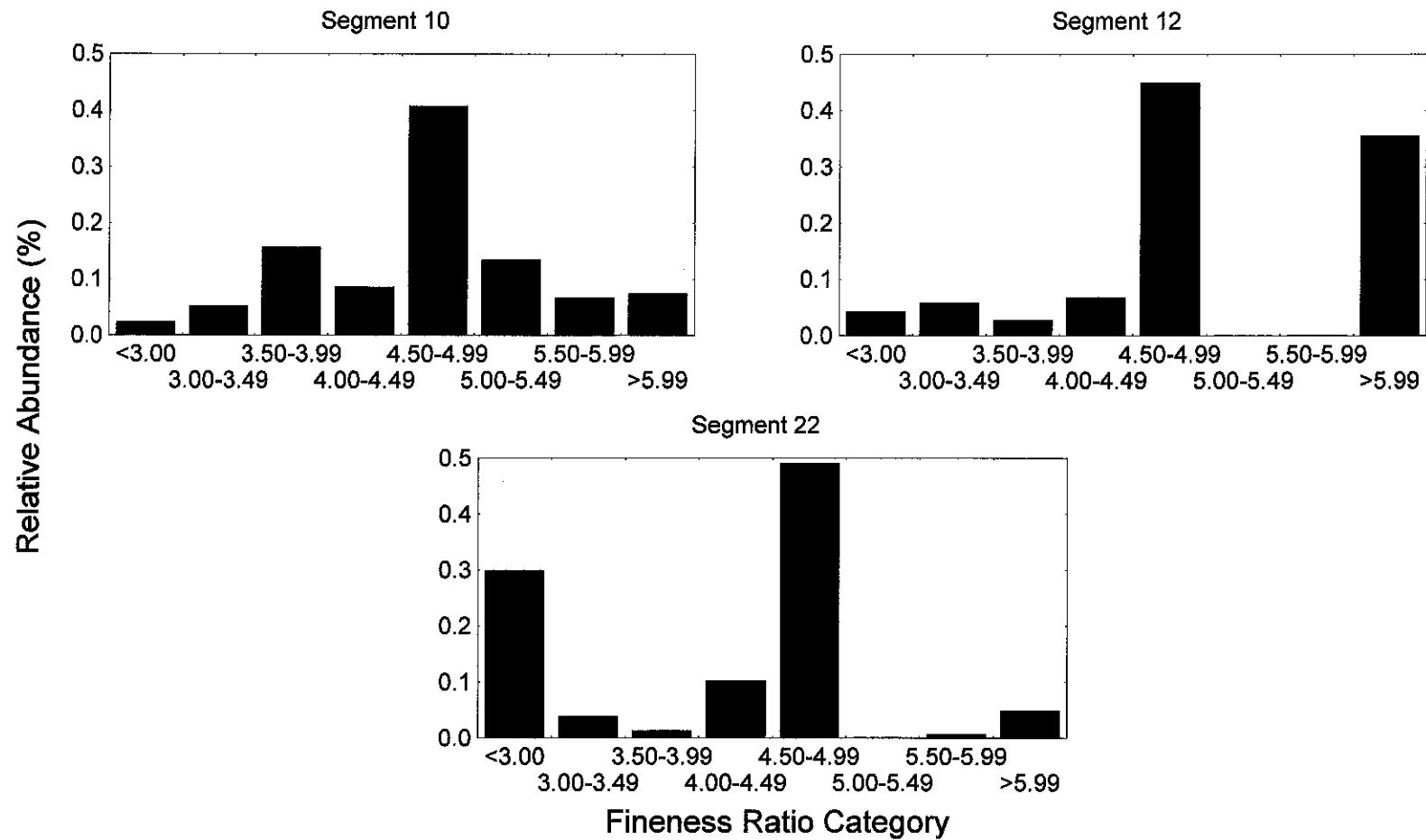
Figure 4.4. Relative abundance of fineness ratio categories in study segments from main channel cross-over, outside bend, and inside bend macrohabitats.
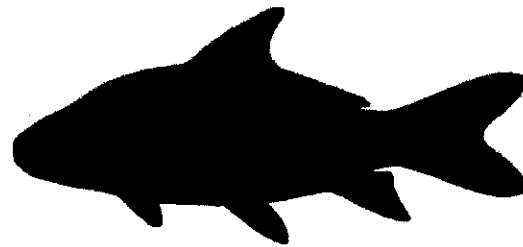
River Carpsucker - FR = 2.70
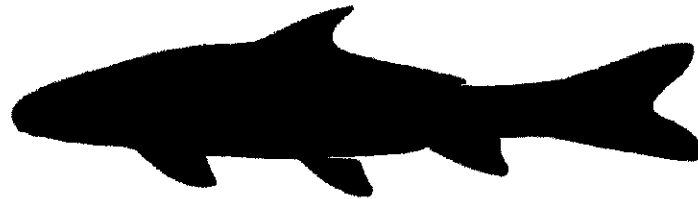
Blue Sucker - FR = 4.57

Sicklefin Chub - FR = 5.24
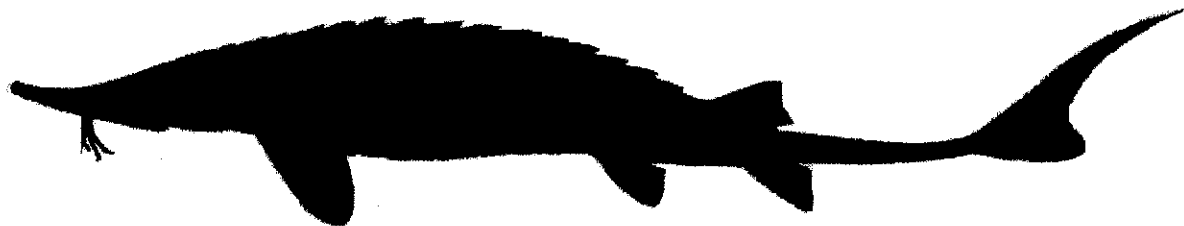
Shovelnose Sturgeon - FR = 8.60

Figure 4.5. Examples of fish body form and fineness ratios from fishes of the Missouri River.
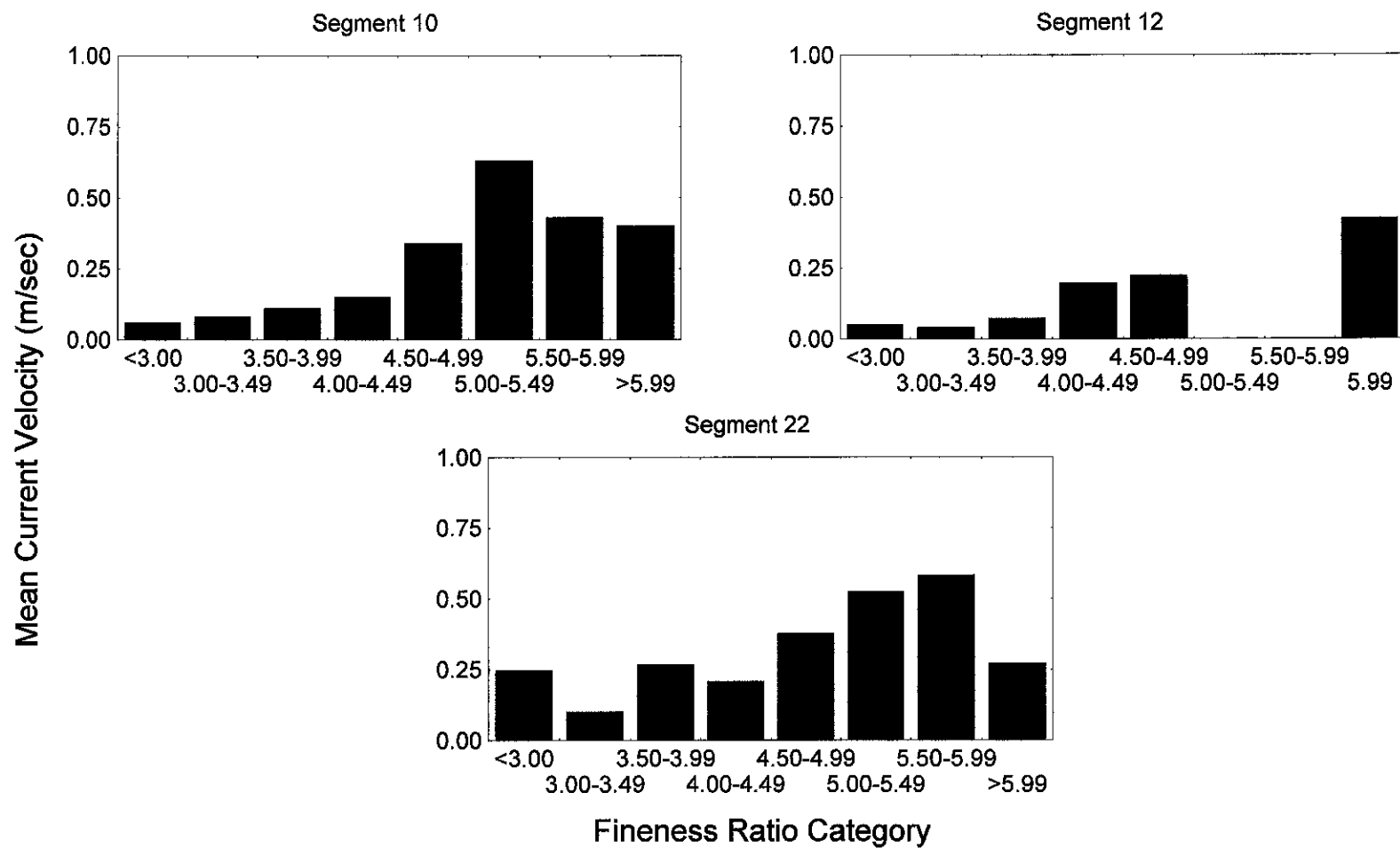
Figure 4.6. Mean current velocity used by fineness ratio categories in study segments.
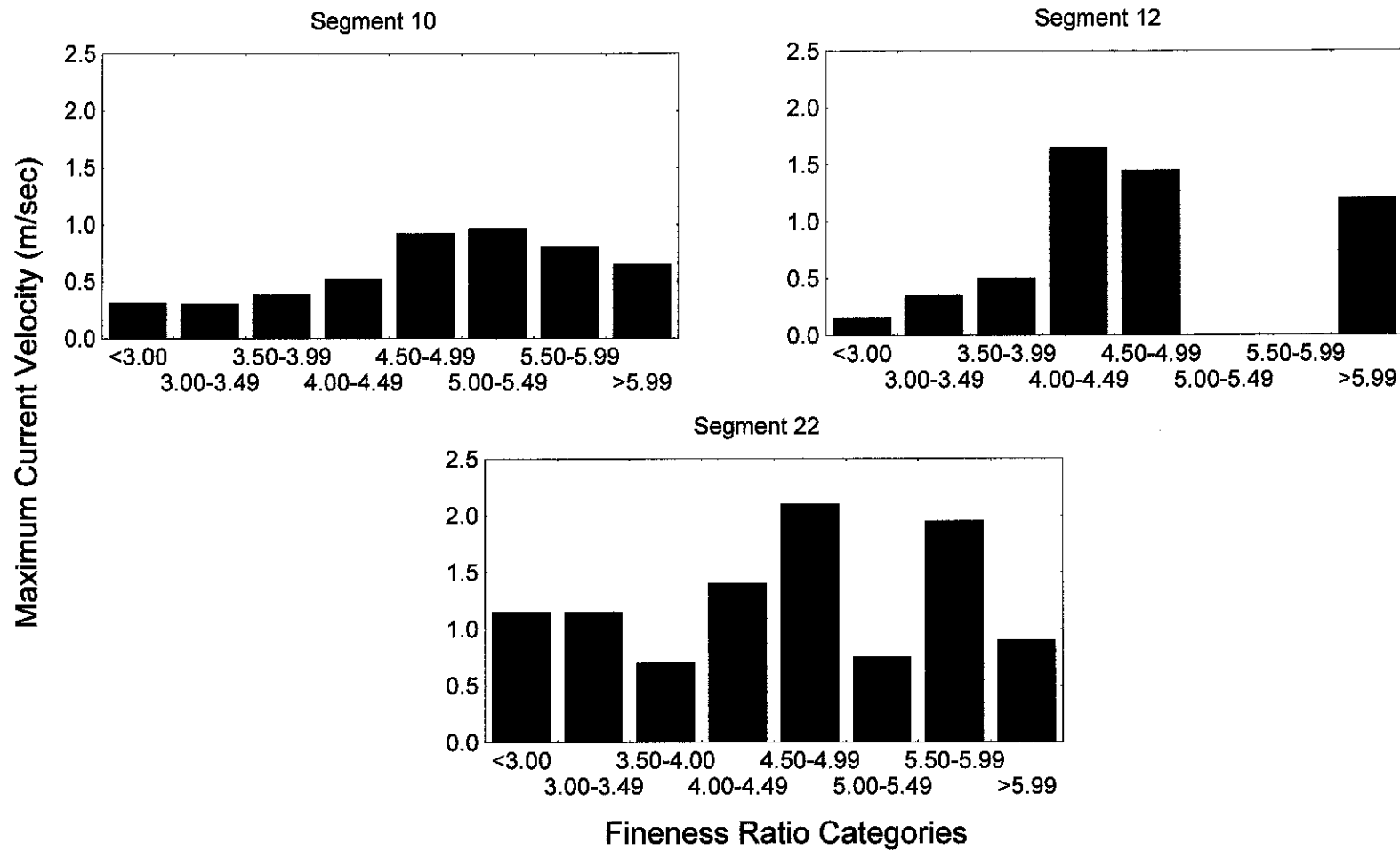
Figure 4.7. Maximum current velocity used by each fineness ratio category in study segments.
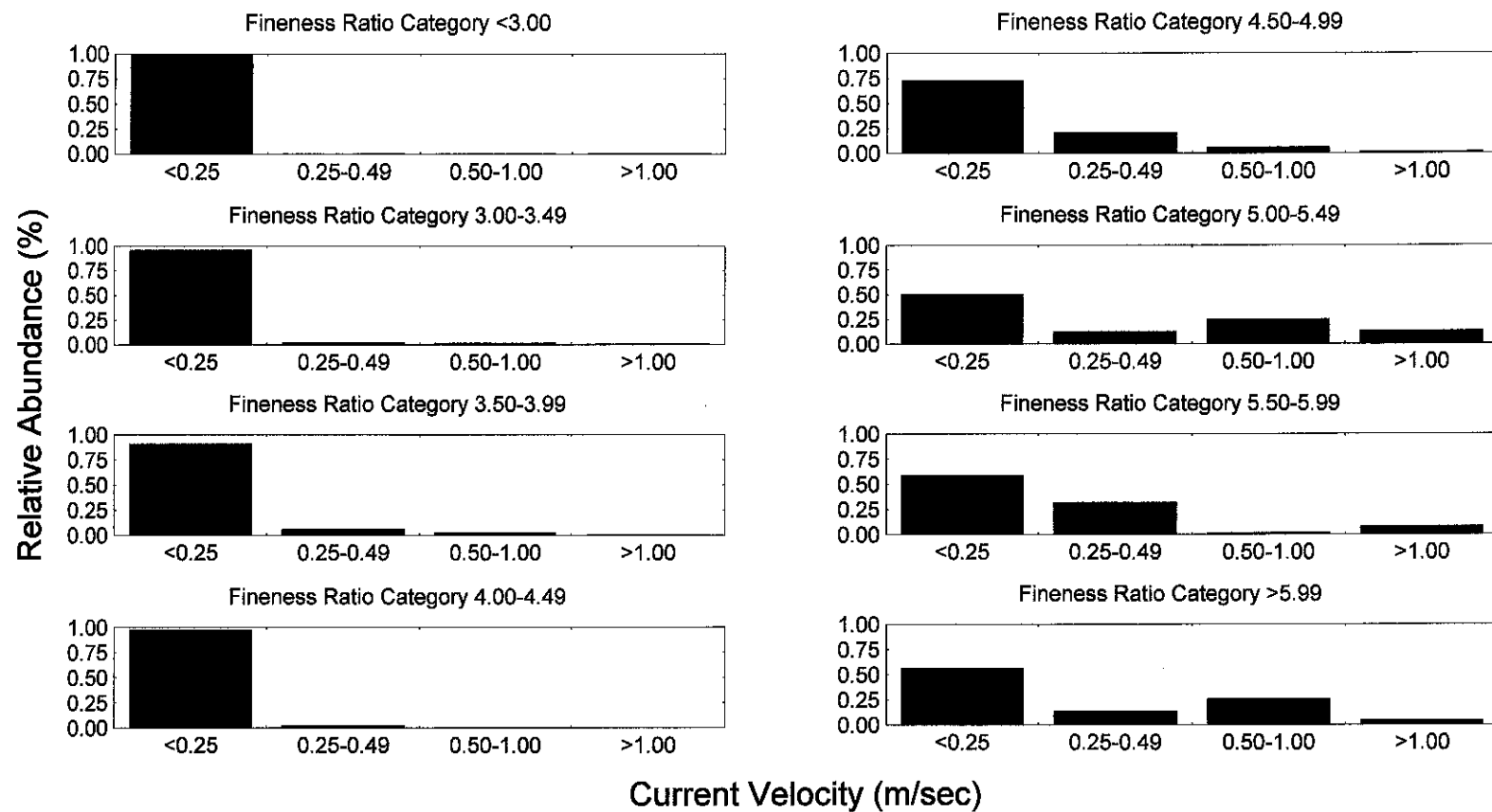
Figure 4.8. Current velocity use by fineness ratio categories in segment 10.
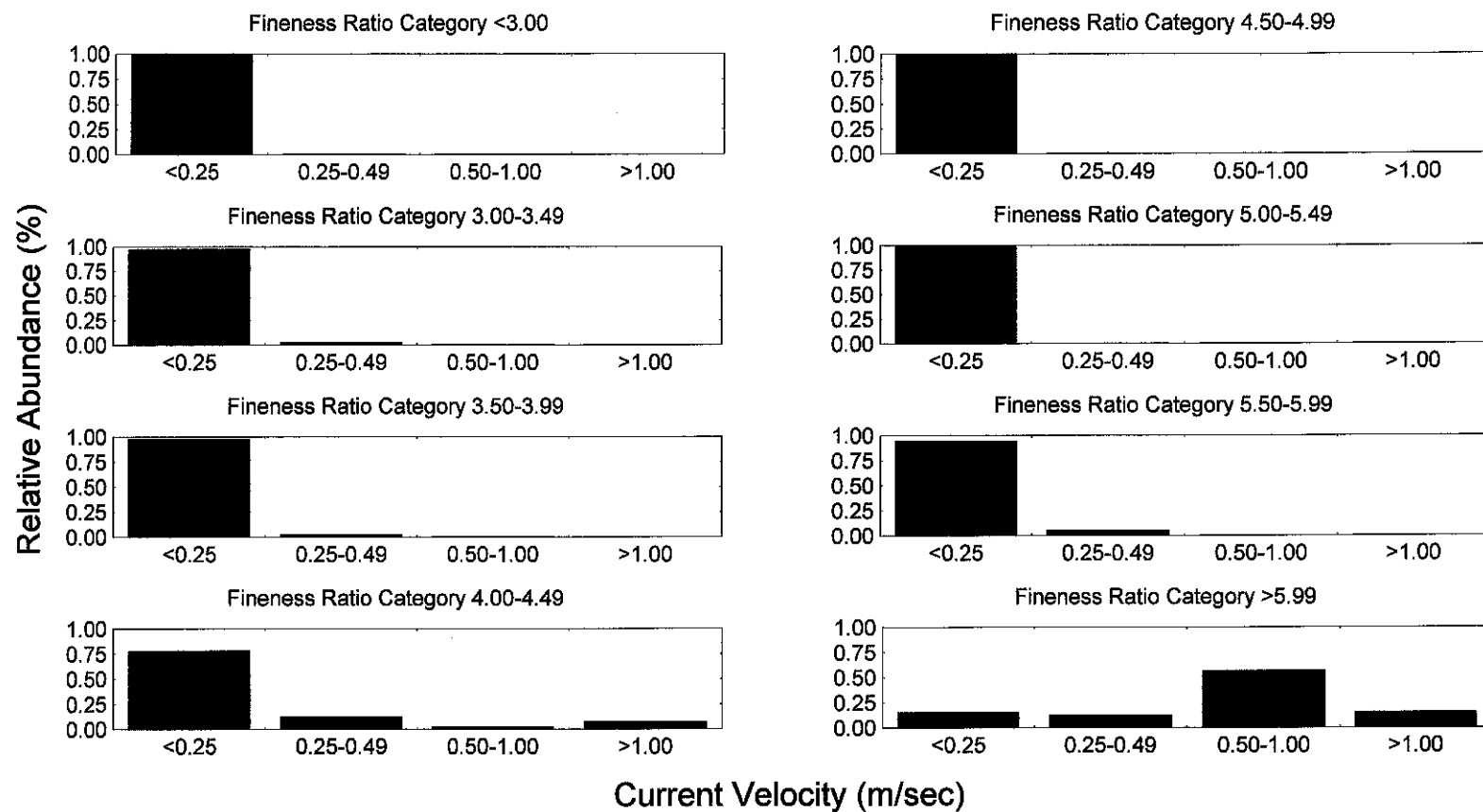
Figure 4.9. Current velocity use by fineness ratio categories in segment 12.
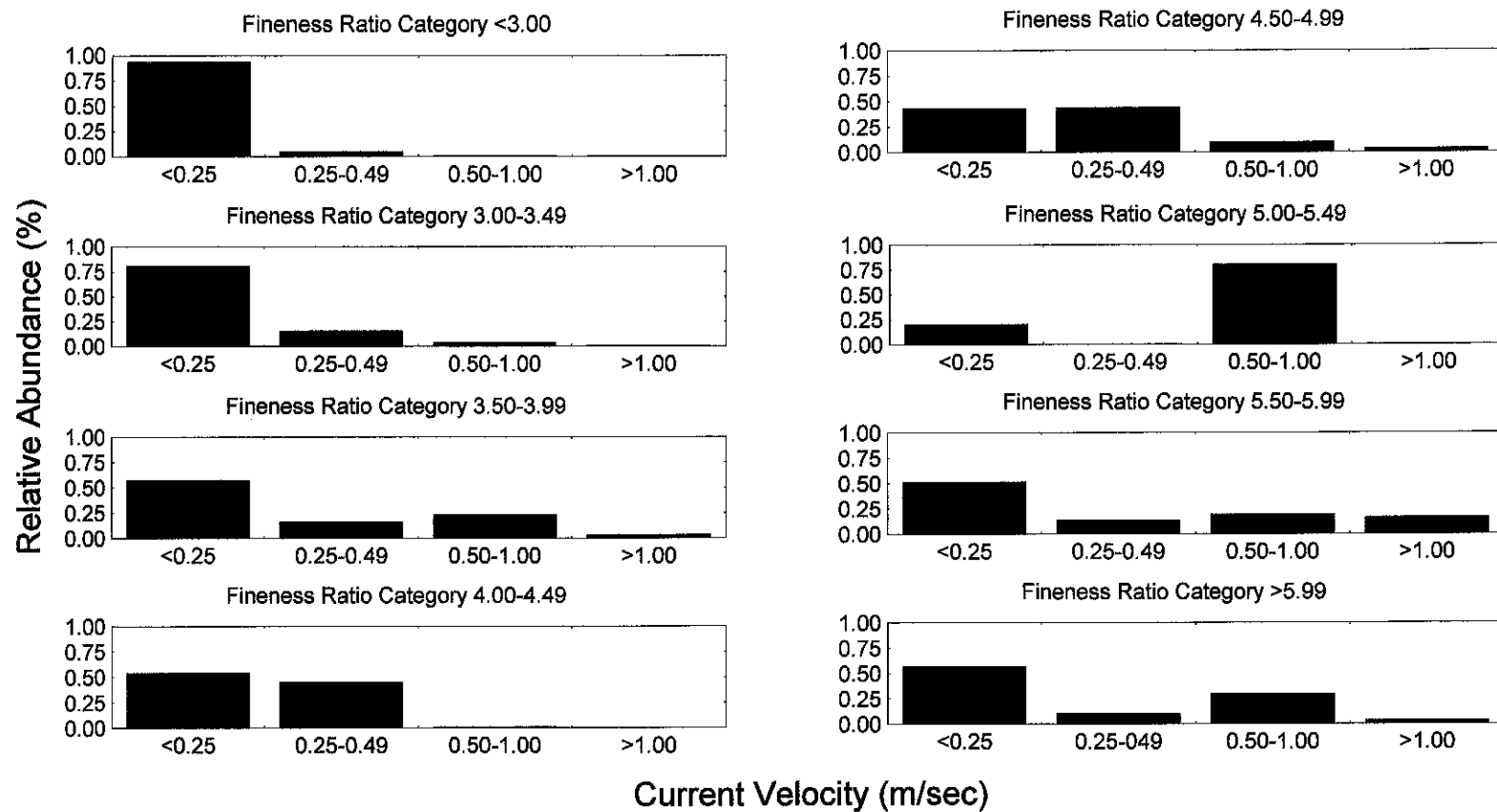
Figure 4.10. Current velocity use by fineness ratio categories in segment 22.
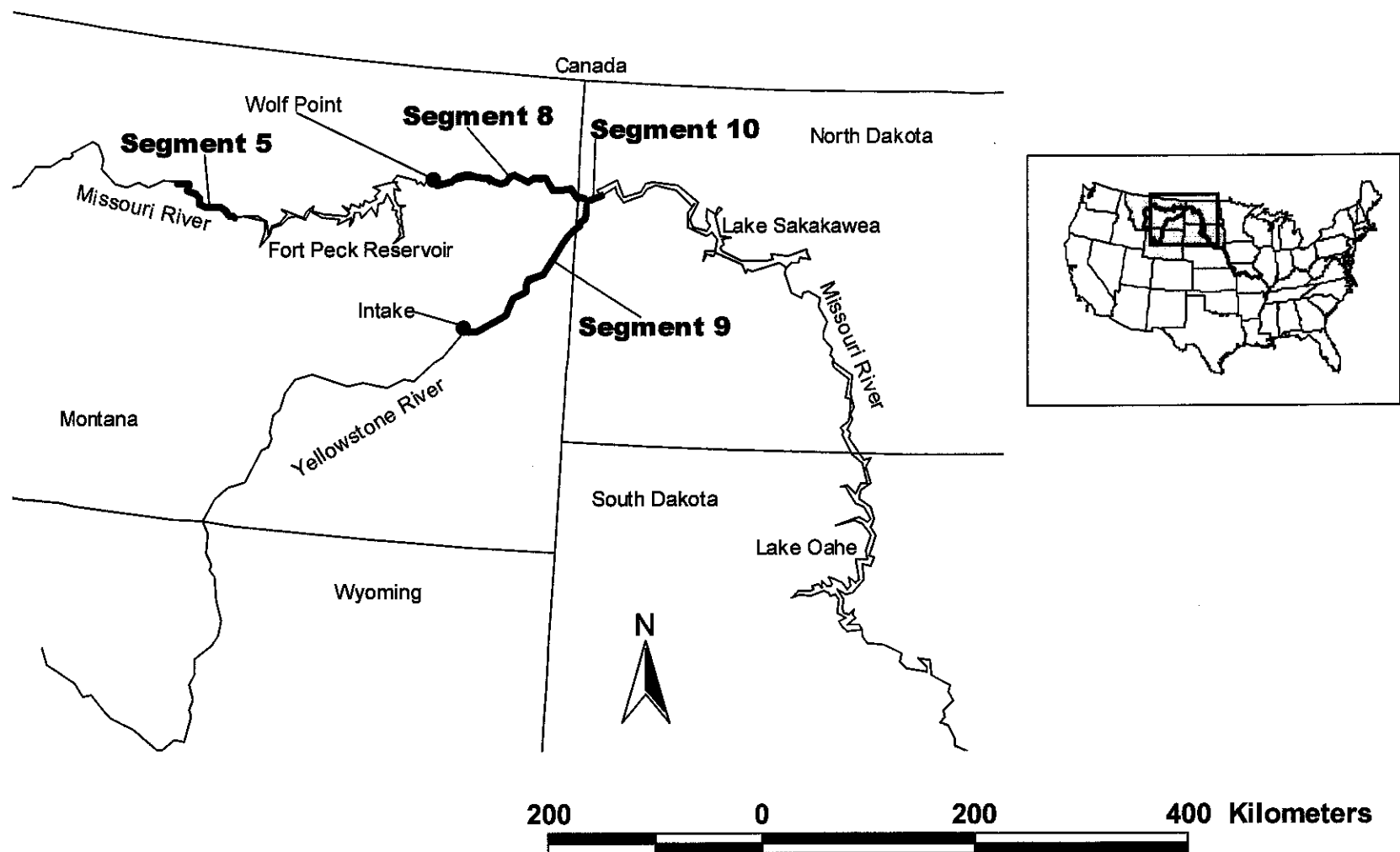
Figure 5.1. Map depicting location of study segments in the Missouri and Yellowstone Rivers.

Figure 5.2. Location of macrohabitats in a typical Missouri River segment.
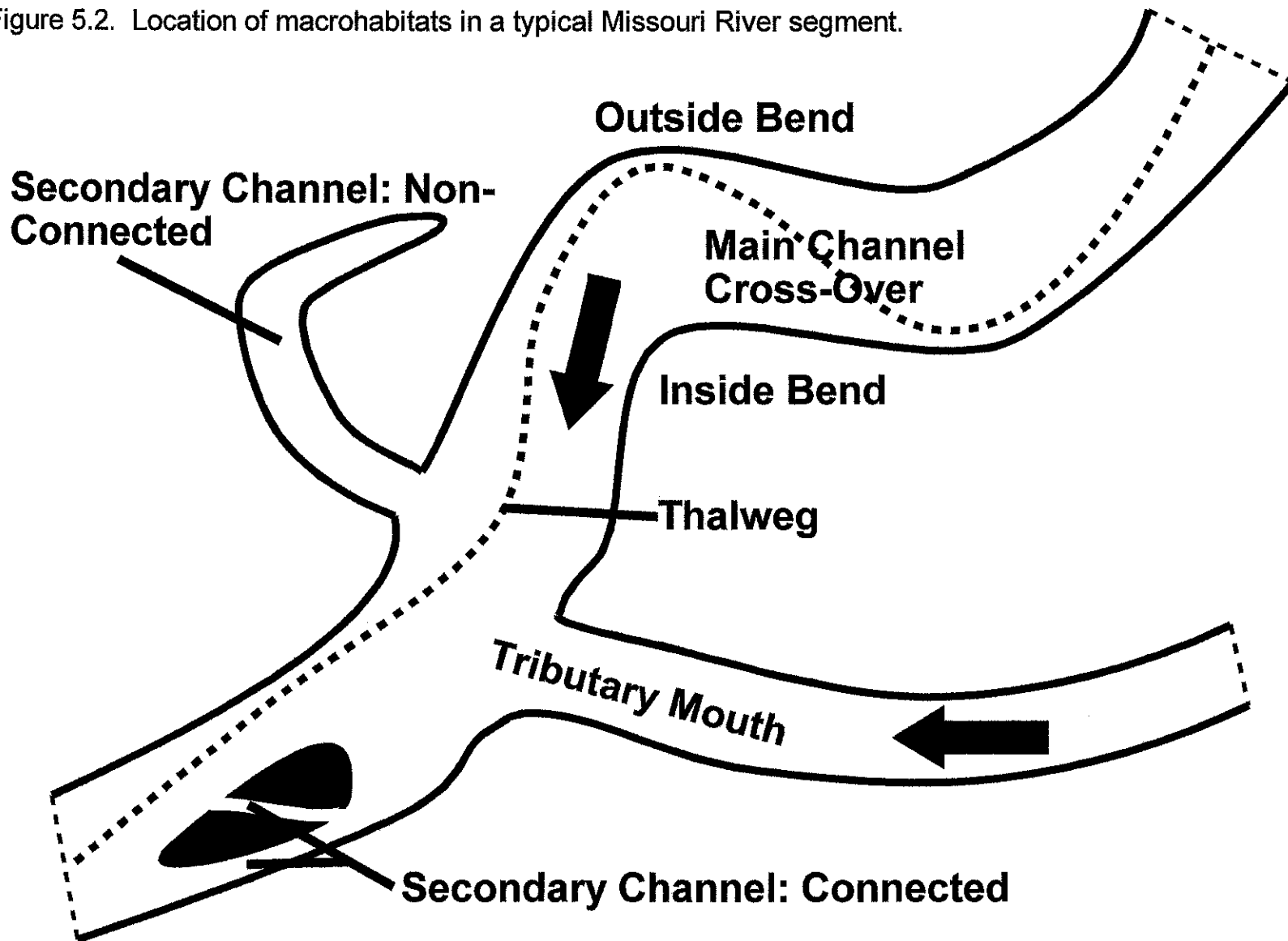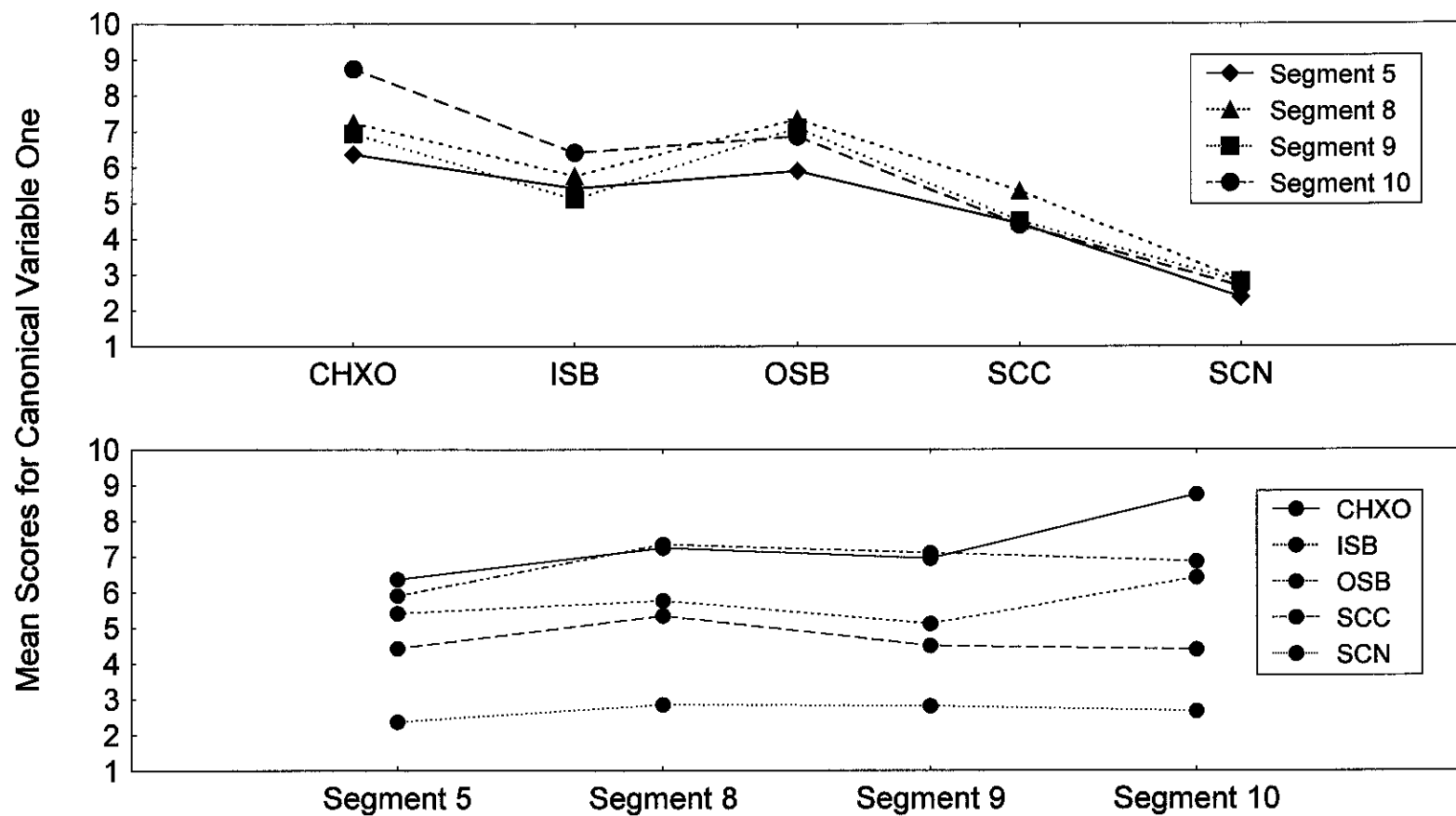
Figure 5.3. Plots of mean canonical scores across segments and macrohabitats (CHXO=main channel cross-over, ISB=inside bend, OSB=outside bend, SCC=secondary channel:connected, SCN=secondary channel: non-connected).
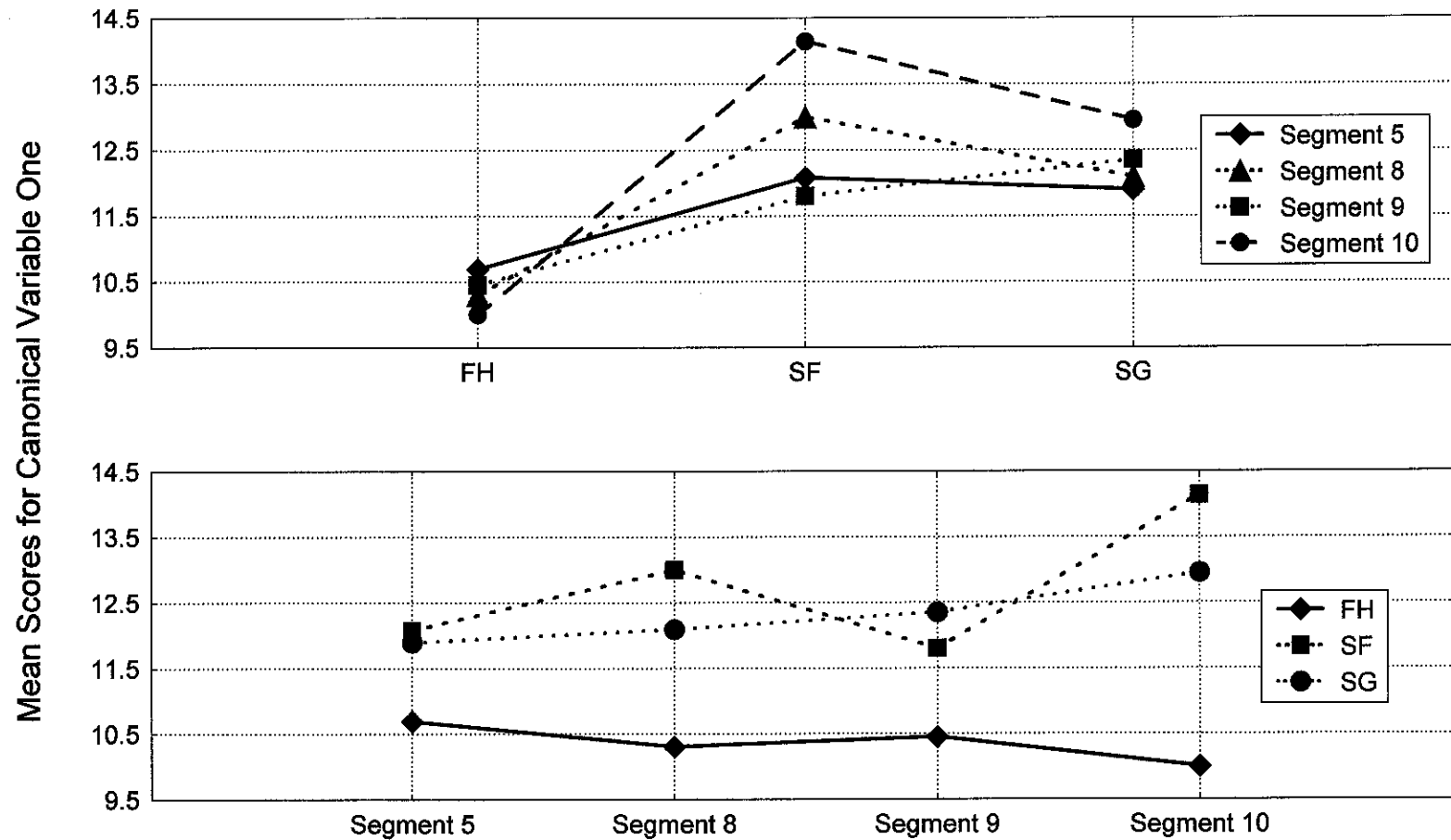
Figure 5.4. Plots of mean canonical scores across segments and species (FH=flathead chub, SF=sicklefin chub, SG=sturgeon chub).
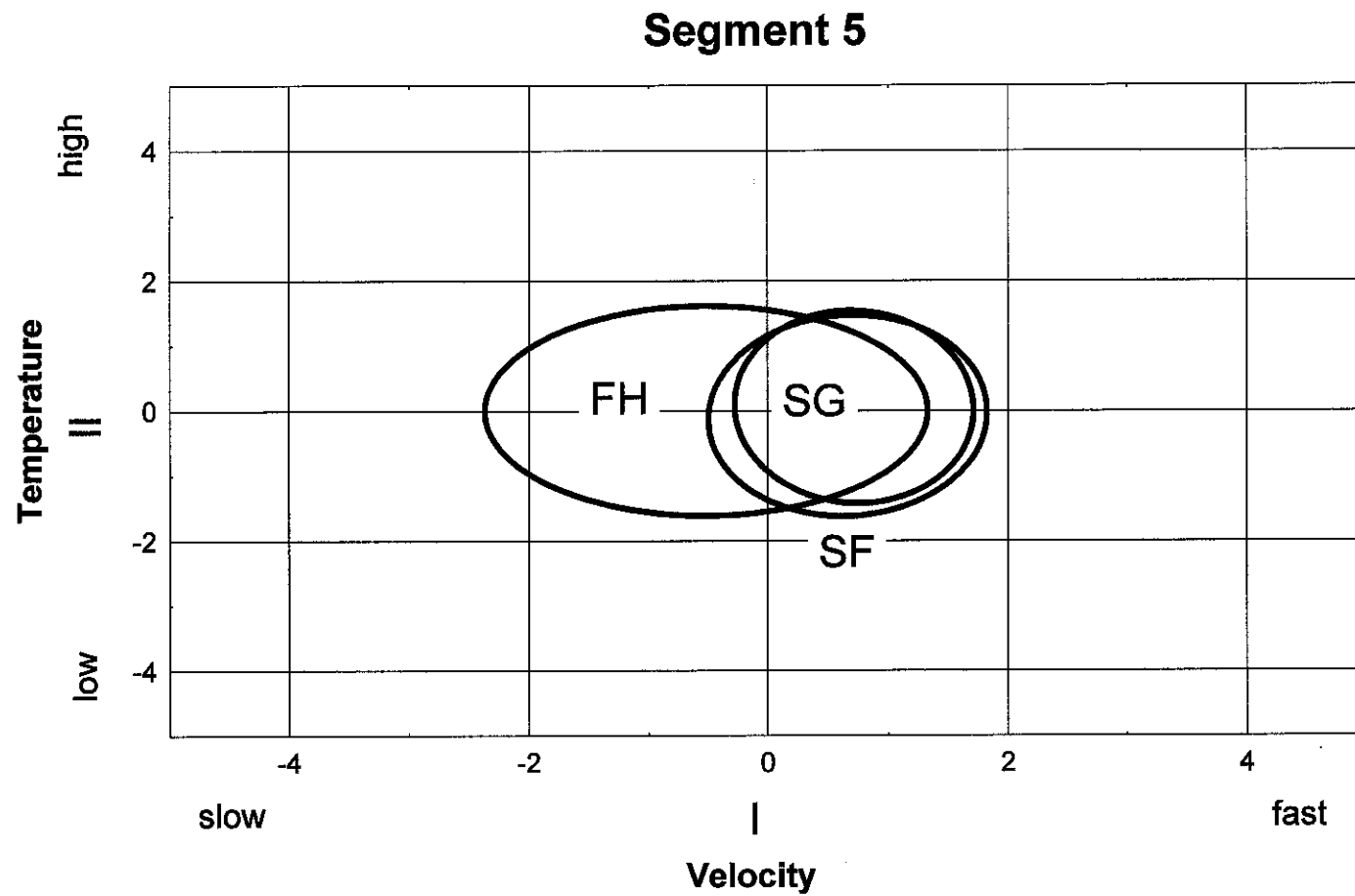
Figure 5.5. Ellipses enclosing 70% of individuals of each cyprinid species in segment 5 plotted on canonical variables I (I) and II (II) (FH=flathead chub, SF=sicklefin chub, SG=sturgeon chub).
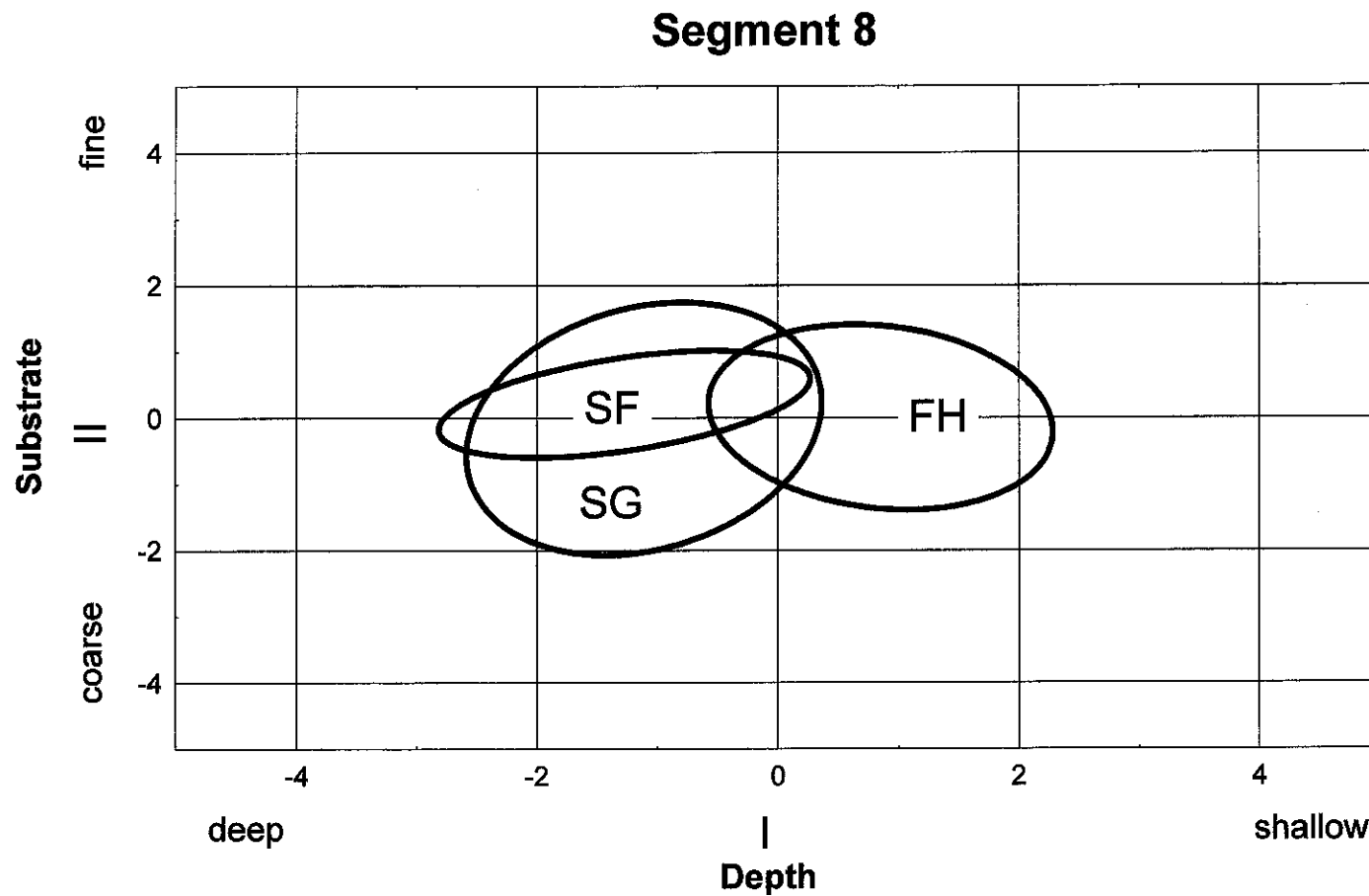
Segment 8

Figure 5.6. Ellipses enclosing 70% of individuals of each cyprinid species in segment 8 plotted on canonical variables I (I) and II (II) (FH=flathead chub, SF=sicklefin chub, SG=sturgeon chub).
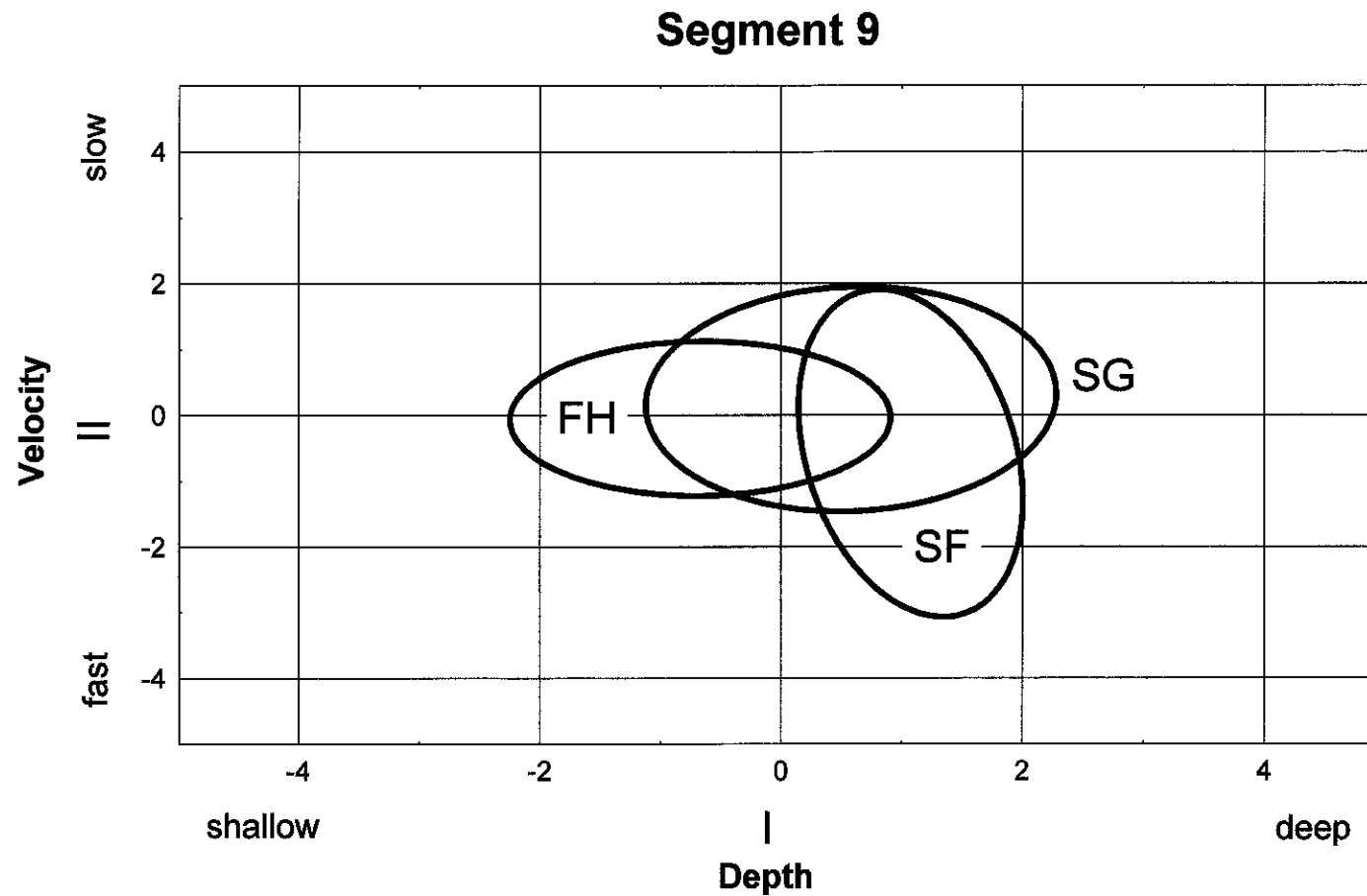
Figure 5.7. Ellipses enclosing 70% of individuals of each cyprinid species in segment 9 plotted on canonical variables I (I) and II (II) (FH=flathead chub, SF=sicklefin chub, SG=sturgeon chub).
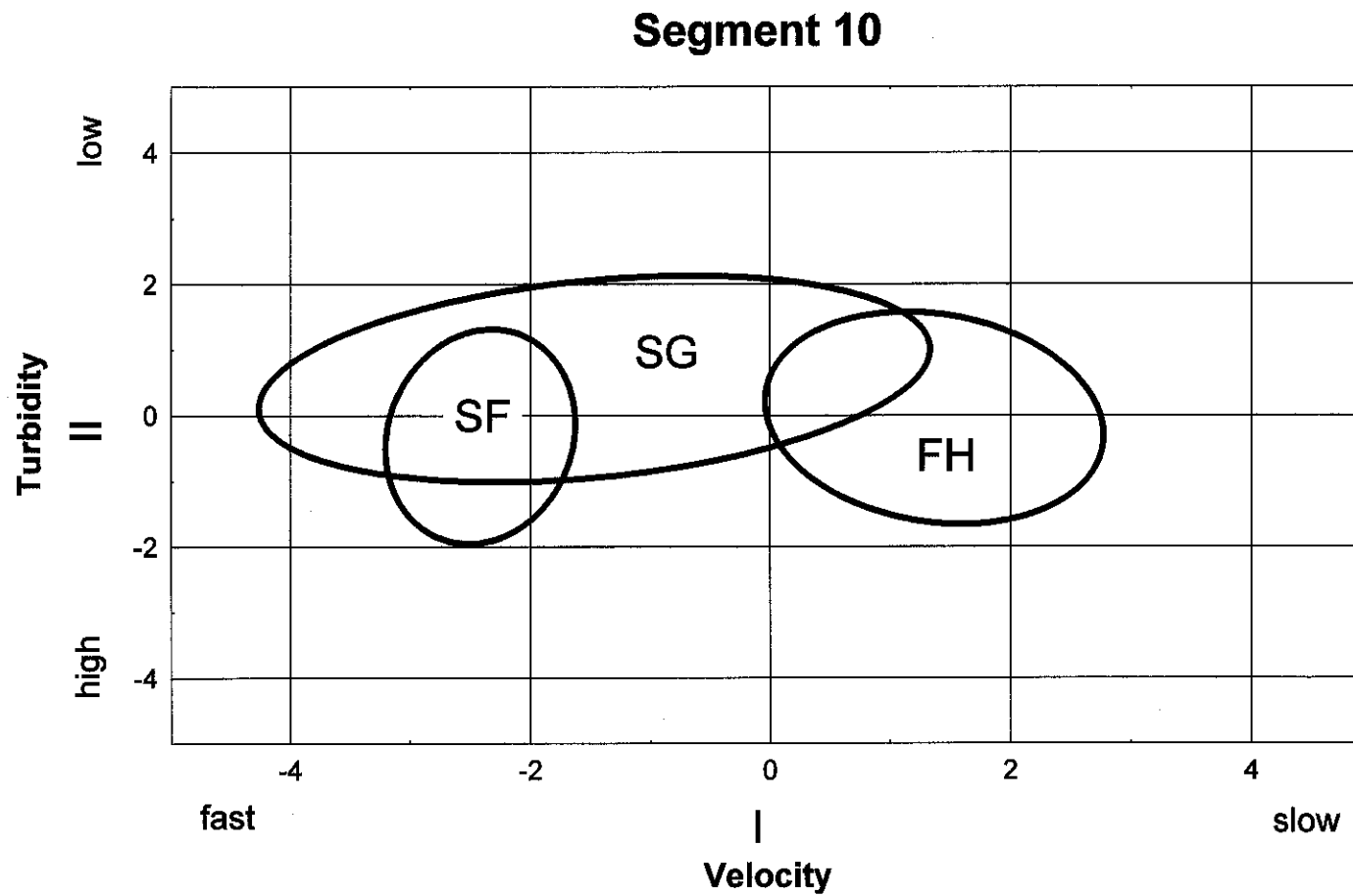
Figure 5.8. Ellipses enclosing 70% of individuals of each cyprinid species in segment 10 plotted on canonical variables I (I) and II (II) (FH=flathead chub, SF=sicklefin chub, SG=sturgeon chub).

APPENDIX B. TABLES

Table 2.1. Relative abundance of prey items (%; equation 2.4) in sucker stomachs in YSS (BM=bigmouth buffalo, RC=river carpsucker, SH=shorthead redhorse, SM=smallmouth buffalo).

Fish Species	N	Prey Items																						
		CY	CA	BS	DP	CD	NA	LP	SI	OS	CH	TR	PD	CP	PS	CX	AD	EP	AG	EB	TY	DT	WM	SD
BM	68	51.3	0.8	29.9	7.8	0.1	0.2	0.5	1.0	<0.1	7.6	-	-	-	-	0.9	-	-	-	-	-	-	-	<0.1
RC	74	37.0	0.5	38.0	9.2	4.2	1.5	0.6	<0.1	0.7	6.4	-	-	-	-	-	<0.1	-	-	-	1.8	-	-	0.1
SH	42	11.8	-	16.7	3.8	2.0	-	-	-	-	47.2	17.0	0.2	1.4	-	-	-	-	-	-	-	-	-	-
SM	92	51.6	0.9	15.0	2.4	7.8	<0.1	<0.1	-	1.6	18.2	-	-	0.1	<0.1	0.1	<0.1	<0.1	-	0.1	-	-	0.1	1.0

(CY=Cyclopoida, CA=Calanoida, BS=Bosminidae, DP=Daphnidae, CD=Chydoridae, NA=Nauplius larvae, LP=Leptidoridae, SI=Sididae, OS=Ostracoda, CH=Chironomidae larvae, TR=Trichoptera larvae, PD=pupae diptera, CP=Chironomidae pupae, PS=Simuliidae pupae, CX=Corixidae, AD=adult diptera, EP=Ephemeroptera larvae, AG=filamentous green algae, EB=Eubranchipus spp., TY=Thysanoptera, DT=organic detritus, WM=water mite, SD=seed).

Table 2.2. Percent surface area of prey items (equation 2.3) in sucker stomachs in YSS (BM=bigmouth buffalo, RC=river carpsucker, SH=shorthead redhorse, SM=smallmouth buffalo).

Fish Species	N	Prey Items																						
		CY	CA	BS	DP	CD	NA	LP	SI	OS	CH	TR	PD	CP	PS	CX	AD	EP	AG	EB	TY	DT	WM	SD
BM	68	45.2	0.9	25.8	10.6	0.1	<0.1	1.5	0.6	<0.1	13.3	-	-	-	-	2.0	-	-	-	-	-	-	-	<0.1
RC	74	31.8	0.9	32.9	15.1	3.6	0.6	0.7	<0.1	0.6	11.8	-	-	-	-	-	0.1	-	-	-	2.0	-	-	<0.1
SH	42	7.1	-	5.6	2.8	0.4	-	-	-	-	57.2	25.2	1.3	0.5	-	-	-	-	-	-	-	-	-	-
SM	92	37.6	0.6	11.9	3.6	3.9	<0.1	<0.1	-	1.1	38.8	-	-	0.1	0.4	0.1	<0.1	<0.1	<0.1	0.1	-	0.0	<0.1	0.5

(CY=Cyclopoida, CA=Calanoida, BS=Bosminidae, DP=Daphnidae, CD=Chydoridae, NA=Nauplius larvae, LP=Leptidoridae, SI=Sididae, OS=Ostracoda, CH=Chironomidae larvae, TR=Trichoptera larvae, PD=pupae diptera, CP=Chironomidae pupae, PS=Simuliidae pupae, CX=Corixidae, AD=adult diptera, EP=Ephemeroptera larvae, AG=filamentous green algae, EB=Eubranchipus spp., TY=Thysanoptera, DT=organic detritus, WM=water mite, SD=seed).

Table 2.3. Frequency of occurrence of prey items (counts; equation 2.5) in sucker stomachs in YSS (BM=bigmouth buffalo, RC=river carpsucker, SH=shorthead redhorse, SM=smallmouth buffalo).

Fish Species	N	Prey Items																						
		CY	CA	BS	DP	CD	NA	LP	SI	OS	CH	TR	PD	CP	PS	CX	AD	EP	AG	EB	TY	DT	WM	SD
BM	68	76.5	11.8	67.6	38.2	5.9	5.9	5.9	2.9	2.9	29.4	-	-	-	-	2.9	-	-	-	-	-	-	-	2.9
RC	74	86.4	11.4	72.7	59.1	27.3	15.9	2.3	2.3	11.4	29.5	-	-	-	-	-	2.3	-	-	-	2.3	-	-	2.3
SH	42	46.2	-	46.2	15.4	23.1	-	-	-	-	92.3	53.9	7.7	15.4	-	-	-	-	-	-	-	-	-	-
SM	92	94.3	13.6	51.1	29.6	39.8	1.1	1.1	-	14.8	54.6	-	-	3.4	1.1	2.3	1.1	1.1	-	1.1	-	-	2.3	10.2

(CY=Cyclopoida, CA=Calanoida, BS=Bosminidae, DP=Daphnidae, CD=Chydoridae, NA=Nauplius larvae, LP=Leptidoridae, SI=Sididae, OS=Ostracoda, CH=Chironomidae larvae, TR=Trichoptera larvae, PD=pupae diptera, CP=Chironomidae pupae, PS=Simuliidae pupae, CX=Corixidae, AD=adult diptera, EP=Ephemeroptera larvae, AG=filamentous green algae, EB=Eubranchipus spp., TY=Thysanoptera, DT=organic detritus, WM=water mite, SD=seed).

Table 2.4. Relative abundance of prey items (%; equation 2.4) in sucker stomachs in GOS (BK=blue sucker, LN=longnose sucker, RC=river carpsucker, SH=shorthead redhorse, WS=white sucker).

Fish Species	N	Prey Items																						
		CY	CA	BS	DP	CD	NA	LP	SI	OS	CH	TR	PD	CP	PL	CX	AD	AG	TD	DT	DM	EP	LC	CT
BK	10	-	-	-	2.8	-	-	-	-	-	73.3	5.4	-	0.9	-	-	-	17.7	-	-	-	-	-	-
LN	74	0.1	<0.1	<0.1	1.9	<0.1	-	-	<0.1	-	18.0	0.4	-	0.5	-	-	0.1	76.4	-	0.8	1.9	-	-	-
RC	84	47.2	1.5	6.3	4.1	8.5	2.7	<0.1	0.5	1.8	20.3	0.2	0.1	0.2	0.1	0.1	0.3	2.7	1.1	0.2	0.2	0.1	0.3	0.7
SH	46	2.5	-	2.2	0.3	3.5	-	-	0.6	-	80.6	2.8	-	2.7	-	-	-	3.6	0.1	0.3	-	-	-	-
WS	71	9.2	0.6	1.6	2.2	5.5	-	1.0	2.1	0.2	44.4	1.0	-	5.3	0.1	-	0.2	15.5	-	8.2	2.4	-	-	0.1

(CY=Cyclopoida, CA=Calanoida, BS=Bosminidae, DP=Daphnidae, CD=Chydoridae, NA=Nauplius larvae, LP=Leptidoridae, SI=Sididae, OS=Ostracoda, CH=Chironomidae larvae, TR=Trichoptera larvae, PD=pupae diptera, CP=Chironomidae pupae, PL=Plecoptera larvae, CX=Corixidae, AD=adult diptera, AG=filamentous green algae, TD= Tardigrada, DT=organic detritus, DM=diatoms, EP=Ephemeroptera larvae, LC=leech, CT=Ceratopogonidae).

Table 2.5. Percent surface area of prey items (equation *2.3*) in sucker stomachs in GOS (BK=blue sucker, LN=longnose sucker, RC=river carpsucker, SH=shorthead redhorse, WS=white sucker).

Fish Species	N	Prey Items																						
		CY	CA	BS	DP	CD	NA	LP	SI	OS	CH	TR	PD	CP	PL	CX	AD	AG	TD	DT	DM	EP	LC	CT
BK	10	-	-	-	2.2	-	-	-	-	-	72.8	7.7	-	0.4	-	-	-	17.0	-	-	-	-	-	-
LN	74	0.0	0.0	0.0	1.9	0.0	-	-	0.0	-	39.9	0.1	-	1.4	-	-	0.1	54.2	-	0.5	1.8	-	-	-
RC	84	34.4	2.4	4.7	7.1	4.7	1.2	0.1	0.2	1.1	35.1	0.2	0.4	0.1	0.1	0.0	0.4	3.6	0.9	0.0	0.1	0.0	0.0	-
SH	46	1.1	-	0.5	0.1	0.5	-	-	1.0	-	87.7	5.9	-	3.2	-	-	-	0.0	0.0	0.0	-	-	-	0.0
WS	71	5.4	0.1	0.2	1.3	1.9	-	0.4	4.5	0.0	61.8	1.9	-	6.7	0.2	-	0.3	9.8	-	4.2	1.2	-	-	0.1

(CY=Cyclopoida, CA=Calanoida, BS=Bosminidae, DP=Daphnidae, CD=Chydoridae, NA=Nauplius larvae, LP=Leptidoridae, SI=Sididae, OS=Ostracoda, CH=Chironomidae larvae, TR=Trichoptera larvae, PD=pupae diptera, CP=Chironomidae pupae, PL=Plecoptera larvae, CX=Corixidae, AD=adult diptera, AG=filamentous green algae, TD= Tardigrada, DT=organic detritus, DM=diatoms, EP=Ephemeroptera larvae, LC=leech, CT=Ceratopogonidae).

Table 2.6. Frequency of occurrence of prey items (counts; equation 2.5) in sucker stomachs in GOS (BK=blue sucker, LN=longnose sucker, RC=river carpsucker, SH=shorthead redhorse, WS=white sucker).

Fish Species	N	Prey Items																						
		CY	CA	BS	DP	CD	NA	LP	SI	OS	CH	TR	PD	CP	PL	CX	AD	AG	TD	DT	DM	EP	LC	CT
BK	10	-	-	-	16.7	-	-	-	-	-	83.3	50.0	-	16.7	-	-	-	33.3	-	-	-	-	-	-
LN	74	5.6	-	-	3.7	1.9	-	-	1.9	-	94.4	1.9	-	40.7	-	-	1.9	90.7	-	1.9	11.1	-	-	-
RC	84	89.7	20.6	44.1	35.3	42.7	16.2	-	1.5	23.5	64.7	2.9	1.5	4.4	1.5	1.5	4.4	4.4	5.9	1.5	1.5	1.5	1.5	-
SH	46	16.7	-	8.3	4.2	16.7	-	-	4.2	-	95.8	20.8	-	4.2	-	-	-	4.2	4.2	4.2	-	-	-	-
WS	71	31.0	4.8	7.1	16.7	19.0	-	2.4	16.7	2.4	92.9	23.8	-	42.9	2.4	-	4.8	23.8	-	2.4	26.2	-	-	2.4

(CY=Cyclopoida, CA=Calanoida, BS=Bosminidae, DP=Daphnidae, CD=Chydoridae, NA=Nauplius larvae, LP=Leptidoridae, SI=Sididae, OS=Ostracoda, CH=Chironomidae larvae, TR=Trichoptera larvae, PD=pupae diptera, CP=Chironomidae pupae, PL=Plecoptera larvae, CX=Corixidae, AD=adult diptera, AG=filamentous green algae, TD= Tardigrada, DT=organic detritus, DM=diatoms, EP=Ephemeroptera larvae, LC=leech, CT=Ceratopogonidae).

Table 2.7. Electivity of prey items (equation 2.7) for suckers in YSS (BM=bigmouth buffalo, RC=river carpsucker, SH=shorthead redhorse, SM=smallmouth buffalo).

Prey Items

Fish Species	Pelagic									Benthic							
	CY	CA	BS	DP	CD	NA	LP	SI	CX	CH	TR	CP	OS	EP	CT	EB	CO
BM	0.08	-0.37	0.23	<0.01	0.01	0.01	0.02	-0.01	0.10	-0.57	-	-0.03	0.01	<0.01	-0.06	-	-0.15
RC	0.08	<0.01	0.13	-0.01	0.05	-0.25	0.01	<0.01	<0.01	-0.51	-	-0.02	-0.14	-0.02	-0.02	-	-0.01
SH	-0.29	-0.01	-0.15	<0.01	-0.02	-0.22	-	-	-	0.13	0.11	0.15	-	-	-0.01	-	-
SM	0.27	0.01	0.07	-0.01	0.13	-0.48	<0.01	-	<0.01	-0.32	-	-0.02	-0.10	-	-0.05	-0.01	-0.15

(CY=Cyclopoida, CA=Calanoida, BS=Bosminidae, DP=Daphnidae, CD=Chydoridae, NA= nauplius larvae, LP=Leptidoridae,SI=Sididae, CX=Corixidae, CH=Chironomidae larvae, TR=Trichoptera larvae, CP=Pupae Chironomidae, OS=Ostracoda, EP=Ephemeroptera larvae, CT=Ceratopogonidae, EB=*Eubranchipus* spp., CO=Chaoboridae).

Table 2.8. Electivity of prey items (equation 2.7) for suckers in GOS (LN=longnose sucker, RC=river carpsucker, SH=shorthead redhorse, WS=white sucker).

Prey Items

Fish Species	Pelagic									Benthic								
	CY	CA	BS	DP	CD	NA	LP	SI	CX	CH	TR	CP	PL	OS	PS	LB	EP	CT
LN	-0.41	-0.02	-0.03	0.13	-	-0.23	-	-	-0.09	0.76	0.23	0.08	-	-	0.22	-	-	-
RC	0.16	-0.01	0.07	-0.04	0.27	-0.27	-0.16	0.50	0.08	0.04	0.04	-0.09	-0.04	0.07	-	-0.13	-0.01	-0.13
SH	-0.26	-0.07	-0.05	-0.04	-0.25	-0.31	-0.20	-	-0.13	0.41	0.13	0.04	-	-	0.04	-	-	0.00
WS	-0.28	-0.01	-0.10	0.14	-0.07	-0.23	0.02	0.05	-	0.30	0.17	0.14	0.03	-	-	-	-	0.04

(CY=Cyclopoida, CA=Calanoida, BS=Bosminidae, DP=Daphnidae, CD=Chydoridae, NA= nauplius larvae, LP=Leptidoridae,SI=Sididae, CX=Corixidae, CH=Chironomidae larvae, TR=Trichoptera larvae, CP=Pupae Chironomidae, PL=Plecoptera Larvae, OS=Ostracoda, PS=Simuliidae pupae, LB=Libellulidae, EP=Ephemeroptera larvae, CT=Ceratopogonidae).

Table 2.9. Food niche overlap (R_o, equation *2.11*) for sucker species in the YSS.

Fish Species	Bigmouth Buffalo	River Carpsucker	Shorthead Redhorse
River Carpsucker	0.94		
Shorthead Redhorse	0.56	0.55	
Smallmouth Buffalo	0.87	0.86	0.74

Table 2.10. Food niche overlap (Ro, equation *2.11*) for sucker species in the GOS.

Fish Species	Longnose Sucker	River Carpsucker	Shorthead Redhorse
River Carpsucker	0.49		
Shorthead Redhorse	0.70	0.79	
White Sucker	0.72	0.80	0.74

Table 2.11. Standardized coefficients of the YSS food categories on the three canonical variables.

Food Category	Canonical Variable I	Canonical Variable II	Canonical Variable III
Cyclopoida	0.1687	0.5377	-0.2662
Bosminidae	0.0460	-0.1540	-0.6330
Daphnidae	-0.0009	-0.2986	-0.5572
Chironomid Larvae	0.7845	0.6580	-0.6279
Chydoridae	-0.0104	0.3654	-0.8818
Trichoptera Larvae	0.9515	-0.2968	-0.1508
Ostracoda	0.2079	-0.2536	-0.3529

Table 2.12. Standardized coefficients of the GOS food categories on the three canonical variables.

Food Category	Canonical Variable I	Canonical Variable II	Canonical Variable III
Cyclopoida	0.4691	-0.4437	0.0518
Bosminidae	0.2882	-0.2295	-0.0711
Daphnidae	0.0082	-0.2558	0.0183
Chironomid Larvae	0.0040	-0.0142	-0.5417
Chydoridae	0.3227	-0.2874	0.1233
Filamentous Algae	-0.6912	-0.6664	-0.0681
Chironomid Pupae	-0.2023	0.3208	0.4589
Trichoptera Larvae	0.0223	0.2623	-0.3084
Organic Detritus	0.0351	0.2068	0.6807

Table 3.1. Species composition and relative abundance in main channel (trawl subsamples=72) and channel border in the ACS (seine subsamples=24).

Species	CATCH			Relative Abundance (%)
	Channel Border Habitat	Main Channel Habitat	Total	
Flathead chub, *Platygobio gracilis*	136	2	138	54.8
Sturgeon chub, *Macrhybopsis gelida*	5	22	27	9.7
Sicklefin chub, *Macrhybopsis meeki*	0	23	23	9.1
Emerald shiner, *Notropis atherinoides*	10	0	10	7.2
River carpsucker, *Carpiodes carpio*	10	0	10	3.4
Shorthead redhorse, *Moxostoma macrolepidotum*	2	0	2	3.2
Western silvery minnow, *Hybognathus argyritis*	18	0	18	2.3
Channel catfish, *Ictalurus punctatus*	1	4	5	2.1
Goldeye, *Hiodon alosoides*	5	0	5	2.1
Sauger, *Stizostedion canadense*	3	0	3	1.9
Spottail shiner, *Notropis hudsonius*	2	0	2	0.8
Unidentified *Stizostedion*	10	0	10	0.7
White sucker, *Catostomus commersonii*	1	0	1	0.6
Stonecat, *Noturus flavus*	3	0	3	0.6
Shovelnose sturgeon, *Scaphirhynchus platorynchus*	2	0	2	0.6
Plains minnow, *Hybognathus placitus*	5	0	5	0.4
Common carp, *Cyprinus carpio*	1	0	1	0.2
Total	214	51	265	100%

Table 3.2. Species composition and relative abundance in main channel (trawl subsamples=72) and channel border in the BCS (seine subsamples=24).

Species	CATCH			Relative Abundance (%)
	Channel Border Habitat	Main Channel Habitat	Total	
Flathead chub, *Platygobio gracilis*	725	0	725	65.1
Western silvery minnow, *Hybognathus argyritis*	168	1	169	9.8
Sicklefin chub, *Macrhybopsis meeki*	3	46	49	8.6
Channel catfish, *Ictalurus punctatus*	19	0	19	5.9
Sturgeon chub, *Macrhybopsis gelida*	7	20	27	1.9
Goldeye, *Hiodon alosoides*	12	0	12	1.3
Unidentified *Stizostedion*	11	0	11	0.9
River carpsucker, *Carpiodes carpio*	104	0	104	0.9
Bigmouth buffalo, *Ictiobus cyprinellus*	12	0	12	0.7
Plains minnow, *Hybognathus placitus*	10	0	10	0.7
Sauger, *Stizostedion canadense*	5	0	5	0.6
Shovelnose sturgeon, *Scaphirhynchus platorynchus*	1	7	8	0.6
Spottail shiner, *Notropis hudsonius*	3	0	3	0.5
Northern pike, *Esox lucius*	3	0	3	0.5
Smallmouth buffalo, *Ictiobus bubalus*	69	0	69	0.4
Brassy minnow, *Hybognathus hankinsoni*	2	0	2	0.2
Walleye, *Stizostedion vitreum*	2	0	2	0.1
Emerald shiner, *Notropis atherinoides*	2	0	2	0.1
Fathead minnow, *Pimephales promelas*	3	0	2	0.1
Freshwater drum, *Aplodinotus grunniens*	3	0	3	0.1
Longnose sucker, *Catostomus catostomus*	1	0	1	0.1
Stonecat, *Noturus flavus*	0	2	2	0.1
White bass, *Morone chrysops*	1	0	1	<0.1
Total	1166	76	1241	100%

Table 3.3. Species composition and relative abundance in main channel (trawl subsamples=72) and channel border in the MZS (seine subsamples=24).

Species	CATCH			Relative Abundance (%)
	Channel Border Habitat	Main Channel Habitat	Total	
Flathead chub, *Platygobio gracilis*	123	2	125	32.7
Goldeye, *Hiodon alosoides*	70	0	70	14.2
Sicklefin chub, *Macrhybopsis meeki*	0	28	28	7.4
River carpsucker, *Carpiodes carpio*	30	0	30	7.2
Channel catfish, *Ictalurus punctatus*	16	14	30	6.5
Emerald shiner, *Notropis atherinoides*	38	0	38	6.3
Western silvery minnow, *Hybognathus argyritis*	29	2	31	5.9
Stonecat, *Noturus flavus*	0	15	15	4.7
Unidentified *Stizostedion*	12	0	12	3.1
Sturgeon chub, *Macrhybopsis gelida*	3	6	9	2.2
Shovelnose sturgeon, *Scaphirhynchus platorynchus*	0	7	7	2.0
Bigmouth buffalo, *Ictiobus cyprinellus*	3	0	3	1.4
Freshwater drum, *Aplodinotus grunniens*	4	0	4	1.2
Northern pike, *Esox lucius*	3	0	3	1.2
Spottail shiner, *Notropis hudsonius*	7	0	7	1.2
Sauger, *Stizostedion canadense*	5	0	5	1.0
Fathead minnow, *Pimephales promelas*	4	0	4	0.3
Smallmouth buffalo, *Ictiobus bubalus*	4	0	4	0.3
Pallid sturgeon, *Scaphirhynchus albus*	0	1	1	0.3
Plains minnow, *Hybognathus placitus*	2	0	2	0.3
Shorthead redhorse, *Moxostoma macrolepidotum*	1	0	1	0.2
Common carp, *Cyprinus carpio*	1	0	1	0.2
Longnose sucker, *Catostomus catostomus*	1	0	1	0.2
Total	356	75	431	100%

Table 3.4. Species composition and relative abundance in main channel (trawl subsamples=72) and channel border in the YRS (seine subsamples=24).

Species	CATCH			Relative
	Channel Border Habitat	Main Channel Habitat	Total	Abundance (%)
Flathead chub, *Platygobio gracilis*	609	14	623	46.4
Goldeye, *Hiodon alosoides*	104	0	104	15.6
Sturgeon chub, *Macrhybopsis gelida*	9	83	92	12.1
Channel catfish, *Ictalurus punctatus*	11	61	72	9.8
Sicklefin chub, *Macrhybopsis meeki*	9	38	47	5.8
Stonecat, *Noturus flavus*	29	0	29	2.5
Western silvery minnow, *Hybognathus argyritis*	40	2	42	2.2
River carpsucker, *Carpiodes carpio*	44	0	44	1.6
Shovelnose sturgeon, *Scaphirhynchus platorynchus*	0	5	5	1.1
Smallmouth buffalo, *Ictiobus bubalus*	21	0	21	1.0
Spottail shiner, *Notropis hudsonius*	1	0	1	0.7
Sauger, *Stizostedion canadense*	4	0	4	0.3
Unidentified *Stizostedion*	2	0	2	0.2
Longnose dace, *Rhinichthys cataractae*	0	1	1	0.2
Fathead minnow, *Pimephales promelas*	2	0	2	0.2
Plains minnow, *Hybognathus placitus*	2	0	2	0.1
Burbot, *Lota lota*	1	0	1	0.1
Common carp, *Cyprinus carpio*	1	0	1	0.1
Bigmouth buffalo, *Ictiobus cyprinellus*	1	0	1	0.1
Emerald shiner, *Notropis atherinoides*	1	0	1	<0.1
Total	891	204	1095	100%

Table 3.5. Species diversity measures for the four study segments. The rarefaction estimates are based on a sample of 200 fish. (ACS=above confluence segment, BCS=below confluence segment, MZS=mixing zone segment, YRS=Yellowstone River segment).

Species Diversity Measures	Segment			
	ACS	BCS	MZS	YRS
Heterogeneity				
Reciprocal of Simpson's Index (1/D, equation *3.4*)	3.05	2.14	6.48	4.25
Richness				
Rarefaction Method	14.63	13.48	18.23	11.82
standard deviation	0.32	1.64	1.44	1.28
Evenness				
Smith and Wilson's Index (E, equation *3.5*)	0.32	0.22	0.26	0.16

Table 3.6. Catch-per-unit-effort for fish species captured with the benthic trawl in main channel habitat (MC) and the bag seine in channel border habitat (CB) in the four study regions (catch expressed as number/100 m2 in MCH and number/m2 in CB; ACS=above confluence study segment, BCS=below confluence study segment, MZS=mixing zone study segment, YRS=Yellowstone River study segment).

	STUDY SEGMENT							
	ACS		BCS		MZS		YRS	
	HABITAT							
SPECIES	CB	MC	CB	MC	CB	MC	CB	MC
STURGEONS, ACIPENSERIDAE								
Pallid sturgeon						<0.1		
Shovelnose sturgeon		<0.1	<0.1	<0.1		0.1		<0.1
MOONEYES, HIODONTIDAE								
Goldeye	0.3		0.3		2.0	<0.1	2.4	
PIKES, ESOCIDAE								
Northern pike			0.1		0.1			
CODS, GADIDAE								
Burbot								<0.1
MINNOWS, CYPRINIDAE								
Brassy minnow			0.1					
Common carp	<0.1				<0.1		<0.1	
Emerald shiner	0.4		<0.1		0.8		<0.1	
Fathead minnow			<0.1		0.1		0.1	
Flathead chub	4.4	<0.1	20.4	<0.1	4.1	<0.1	18.0	<0.1
Longnose dace								<0.1
Plains minnow	0.2		0.3		0.1		0.1	
Sicklefin chub		0.2	0.1	0.3		0.2		0.4
Spottail shiner	0.1		<0.1	<0.1	0.2		0.0	
Sturgeon chub	0.1	0.1	0.2	0.2	0.1	<0.1	0.3	0.7
Western silvery minnow	0.6		4.4	<0.1	1.1	<0.1	1.1	<0.1
SUCKERS, CATOSTOMIDAE								
Bigmouth buffalo			0.4		0.1		<0.1	
Longnose sucker			<0.1		<0.1			
River carpsucker	0.5		1.0		1.5	<0.1	1.2	
Shorthead redhorse	0.2				<0.1			
Smallmouth buffalo			0.2		0.1		0.6	
White sucker	<0.1							
BULLHEAD CATFISHES, ICTALURIDAE								
Channel catfish	0.1	<0.1	0.1	0.1	0.5	0.1	0.3	0.6
Stonecat		<0.1	<0.1			0.1		0.3

Table 3.6. Continued.

SPECIES	STUDY SEGMENT							
	ACS		BCS		MZS		YRS	
	HABITAT							
	CB	MC	CB	MC	CB	MC	CB	MC
TEMPERATE BASSES, PERCICHTHYIDAE								
White bass			0.0					
PERCHES, PERCIDAE								
Sauger	0.1		0.1		0.1	<0.1	0.1	
Unidentifiable *Stizostedion spp.*	0.2		0.3		0.4		0.1	
Walleye			0.0					
DRUMS, SCIAENIDAE								
Freshwater drum			0.1		0.1			

Table 3.7. Physiochemical characterization (mean, range, standard deviation(SD)) of channel border habitat.

Physiochemical Variable	Segment			
	Above Confluence	Below Confluence	Mixing Zone	Yellowstone River
Mean Depth (m)	0.4	0.3	0.5	0.5
Range	0.2-0.7	0.1-0.8	0.2-0.8	0.2-0.9
SD	0.2	0.2	0.2	0.2
Mean Current Velocity (m/s)	0.2	0.1	0.2	0.1
Range	0.0-0.4	0.0-0.4	0.0-0.4	0.0-0.5
SD	0.1	0.1	0.1	0.1
Mean Turbidity (NTU)	144.3	179.4	183.5	167.0
Range	57.0-306.0	38.0-326.0	21.0-423.3	30.0-673.0
SD	77.8	93.0	126.9	150.4
Mean Temperature (Celsius)	20.2	21.4	22.0	21.7
Range	18.4-23.0	16.3-25.4	18.1-25.5	17.8-24.5
SD	1.5	2.5	2.4	1.8
Substrate Composition (%)				
Silt	66.8	37.3	68.7	38.3
Sand	33.2	62.4	31.2	61.7
Gravel	0.0	0.3	0.1	0.0

Table 3.8. Physiochemical characterization (mean, range, standard deviation(SD)) of main channel habitat.

Physiochemical Variable	Segment			
	Above Confluence	Below Confluence	Mixing Zone	Yellowstone River
Mean Depth (m)	3.7	3.9	5.4	4.0
Range	1.2-6.2	0.9-7.2	2.3-8.5	2.1-6.2
SD	1.2	1.5	1.6	1.2
Mean Current Velocity (m/s)	1.0	1.1	1.1	0.9
Range	0.6-1.7	0.5-1.5	0.4-1.7	0.5-1.2
SD	0.2	0.2	0.3	0.2
Mean Turbidity (NTU)	122.0	188.9	239.4	224.1
Range	46.0-423.0	41.0-522.0	24.0-969.0	21.0-605.0
SD	93.4	113.0	266.9	200.9
Mean Temperature (Celsius)	19.0	20.9	21.0	21.6
Range	13.9-21.5	16.3-25.4	15.1-27.6	18.1-24.5
SD	2.0	2.1	2.9	1.8
Substrate Composition (%)				
Silt	6.6	<0.1	5.3	2.7
Sand	91.4	97.2	91.0	90.9
Gravel	1.9	2.5	3.7	6.4

Table 3.9. Results of canonical analysis of variates and ANOVA performed on main channel habitat physiochemical data.

Water Physiochemical Category	Canonical Variable I	Canonical Variable II	Canonical Variable III	Probability Value for ANOVA F-test
Depth	-0.9808	0.5062	0.1755	0.0001
Velocity	0.3862	-1.0538	0.5950	0.0001
Turbidity	-0.1773	0.3926	0.0638	0.1145
Temperature	-0.3730	-0.8016	-0.5918	0.2195
Percent Silt	0.1584	0.4280	0.1035	0.0001
Percent Sand	0.2853	-0.0961	-0.0548	0.0001

Table 3.10. Results of canonical analysis of variates and ANOVA performed on channel border habitat physiochemical data.

Water Physiochemical Category	Canonical Variable I	Canonical Variable II	Canonical Variable III	Probability Value for ANOVA F-test
Depth	0.8003	-0.5134	-0.6702	0.0087
Velocity	-0.5474	0.4682	-0.2191	0.6913
Turbidity	-0.0231	0.3412	0.1542	0.7798
Temperature	0.5679	-0.4578	0.7251	0.0991
Percent Silt	0.2761	0.7803	0.5028	0.0073
Percent Sand	-0.2909	-0.1241	0.1083	0.0136

Table 3.11. Results of species presence/absence canonical analysis of variates and ANOVA performed on physiochemical variables.

Species Environmental Variable	Canonical Analysis Standardized Coefficients	Probability Value for ANOVA F-test
Flathead Chub*		
Depth/Veloctiy Principal Component	-0.9283	**0.0001**
Turbidity (NTU)	0.0338	0.3744
Temperature (°C)	0.0175	0.0629
Percent Silt	0.2691	**0.0001**
Percent Sand	0.0272	**0.0001**
Invertebrate Drift (number/liter)	0.0666	0.2954
Discharge (m^3/sec)	0.1996	0.8518
Sicklefin Chub*		
Depth/Veloctiy Principal Component	-0.5430	**0.0007**
Turbidity (NTU)	-0.1186	0.0626
Temperature (°C)	-0.4181	**0.0167**
Percent Silt	1.0382	**0.0001**
Percent Sand	0.7180	**0.0002**
Invertebrate Drift (number/liter)	-0.0868	0.3820
Discharge (m^3/sec)	0.6711	**0.0023**
Sturgeon Chub*		
Depth/Veloctiy Principal Component	-0.1001	0.9823
Turbidity (NTU)	-0.1278	0.2397
Temperature (°C)	-0.0270	0.9076
Percent Silt	-1.0895	**0.0351**
Percent Sand	-0.6679	0.0675
Invertebrate Drift (number/liter)	-0.0058	0.3977
Discharge (m^3/sec)	-0.8731	**0.0001**
Western Silvery Minnow*		
Depth/Veloctiy Principal Component	-0.9782	**0.0001**
Turbidity (NTU)	0.0602	0.2950
Temperature (°C)	-0.1942	0.9305
Percent Silt	0.0605	**0.0001**
Percent Sand	-0.0752	**0.0001**
Invertebrate Drift (number/liter)	-0.0653	0.5257
Discharge (m^3/sec)	0.0837	0.4731

Asterisk (*) next to species indicates significant Wilk's Lambda for presence/absence MANOVA **bold** indicates significance at $P<0.05$

Table 3.12. Model equations for characterizing habitat where flathead chub, sicklefin chub, sturgeon chub, and western silvery minnow were present (1, number, or CPUE) or absent (0) (pc=principal component).

Species	Model Equation	R^2	P-value
Logistic Regression			
Flathead Chub	Log odds of fish presence=-1.6079-2.0391(depth/velocity pc)		<0.0001
Sicklefin Chub	Log odds of fish presence=-1.3714+0.5901(temperature)+0.4063(% sand)-0.9228(discharge)+0.6121(depth/velocity pc)		<0.0001
Sturgeon Chub	Log odds of fish presence=-1.2986+0.3113(% sand)-1.0122(discharge)		<0.0001
Western Silvery Minnow	Log odds of fish presence=-2.5772-1.3660(depth/velocity pc)+0.0392(% sand)		<0.0001
Poisson Regression			
Sicklefin Chub	Log number of fish=-0.8321-2.3174(current velocity)+0.1404(temperature)	0.32	<0.0001
Sturgeon Chub	Log number of fish=2.4702-0.0001(discharge)+0.0228(% gravel)-0.0021(turbidity)-0.8707(current velocity)	0.55	<0.0001
Western Silvery Minnow	Log number of fish=-5.1597+0.0321(effort)-6.3980(current velocity)+0.0293(%sand)+0.0053(benthic invertebrate density)	0.43	<0.0001
Linear Least-squares Regression			
Flathead Chub	Fish catch-per-unit-effort=0.1370-0.3350(current velocity)+0.0003(turbidity)+0.0021(% sand)+0.000982(benthic invertebrate density)	0.47	<0.0001

Table 3.13. Predictive success of logistic models developed for flathead chub, sicklefin chub, sturgeon chub, and western silvery minnow.

Flathead Chub	Predicted		
		Present	Absent
Observed	Present	27 (90%)	3 (10%)
	Absent	0 (0%)	30 (100%)

Percent classified correctly   <u>95%</u>

Sicklefin Chub	Predicted		
		Present	Absent
Observed	Present	21 (70%)	9 (30.0%)
	Absent	3 (10%)	27 (90%)

Percent classified correctly   <u>80%</u>

Sturgeon Chub	Predicted		
		Present	Absent
Observed	Present	17 (57%)	13 (43%)
	Absent	14 (47%)	16 (53%)

Percent classified correctly   <u>55%</u>

Western Silvery Minnow	Predicted		
		Present	Absent
Observed	Present	29 (97%)	1 (3%)
	Absent	11 (37%)	19 (63%)

Percent classified correctly   <u>80%</u>

Table 3.14. Results of canonical analysis of variates and ANOVA performed on flathead chub, sicklefin chub, sturgeon chub, and western silvery minnow habitat use data. A significant F-test for a physiochemical variable indicates differential use of the variable among the four species.

Water Physiochemical Category	Canonical Variable I	Canonical Variable II	Canonical Variable III	Probability Value for ANOVA F-test
Depth	-0.1851	-0.4651	-0.9243	0.0001
Velocity	-0.6854	0.6082	0.6310	0.0001
Turbidity	-0.0594	0.4293	0.0862	0.1145
Temperature	0.0952	0.6362	-0.5245	0.2195
% Silt	0.4587	0.2542	-1.2828	0.0001
% Sand	0.1001	-0.2883	-1.4582	0.0001

Table 4.1. Species relative abundance (rel. abun.) as a fraction of 1.00 in segment 10 macrohabitats (CHXO=main channel cross-over, ISB=inside bend, OSB=outside bend, SCC=secondary channel: non-connected, SCN=secondary channel: connected, TRM=tributary mouth).

MACROHABITAT

SPECIES	CHXO	ISB	OSB	SCC	SCN	TRM	Total	Combined Rel. Abun. All Macrohabitats	Combined Rel. Abun. CHXO, ISB, OSB
STURGEONS; ACIPENSERIDAE									
Shovelnose sturgeon, *Scaphirhynchus platorynchus*	0.18	0.13	0.33	0.05		0.31	1.00	0.01	0.04
MOONEYES; HIODONTIDAE									
Goldeye, *Hiodon alosoides*	0.01	0.08	0.15	0.26	0.43	0.08	1.00	0.16	0.16
PIKES; ESOCIDAE									
Northern pike, *Esox lucius*		0.04	0.07	0.09	0.76	0.04	1.00	0.02	<0.01
CODS; GADIDAE									
Burbot, *Lota lota*		0.00	0.85	0.03	0.09	0.03	1.00	0.01	0.04
MINNOWS; CYPRINIDAE									
Common carp, *Cyprinus carpio*	0.03	0.03	0.32	0.13	0.46	0.03	1.00	0.02	0.01
Common carp < 150 mm, *Cyprinus carpio*		0.03		0.04	0.93		1.00	0.10	0.01
Emerald shiner, *Notropis atherinoides*		0.14	0.41	0.07	0.37	0.01	1.00	0.03	0.06
Flathead chub, *Platygobio gracilis*	0.01	0.43	0.08	0.43	<0.01	0.05	1.00	0.24	0.37
Sicklefin chub, *Macrhybopsis meeki*	0.18	0.18	0.55	0.05		0.05	1.00	0.01	0.03
Spottail shiner, *Notropis hudsonius*		0.06	0.63	0.19	0.13		1.00	0.01	0.01
Sturgeon chub, *Macrhybopsis gelida*	0.05	0.57	0.29	0.10			1.00	0.01	0.03
Western silvery minnow, *Hybognathus argyritis*		0.25	0.06	0.62	0.05	0.03	1.00	0.13	0.07
SUCKERS; CATOSTOMIDAE									
Bigmouth buffalo, *Ictiobus cyprinellus*		0.06		0.09	0.85		1.00	0.10	0.01
River carpsucker, *Carpiodes carpio*					0.85	0.15	1.00	0.01	
River carpsucker < 150 mm, *Carpiodes carpio*		0.15		0.28	0.48	0.09	1.00	0.01	0.01
Shorthead redhorse, *Moxostoma macrolepidotum*			0.15	0.09	0.76		1.00	0.01	<0.01
Smallmouth buffalo, *Ictobius bubalus*					1.00		1.00	0.01	
Smallmouth buffalo < 150 mm, *Ictobius bubalus*		0.36		0.23	0.41		1.00	0.03	0.03
BULLHEAD CATFISHES; ICTALURIDAE									
Channel catfish, *Ictalurus punctatus*	0.04	0.10	0.23		0.37	0.27	1.00	0.04	0.04
Stonecat, *Noturus flavus*	0.05	0.05	0.90				1.00	0.01	0.02

Table 4.1. Continued.

| SPECIES | MACROHABITAT | | | | | | Total | Combined Rel. Abun. All Macrohabitats | Combined Rel. Abun. CHXO, ISB, OSB |
	CHXO	ISB	OSB	SCC	SCN	TRM			
PERCHES; PERCIDAE									
Sauger, *Stizostedion canadense*			0.64	0.03	0.33		1.00	0.02	0.04
Walleye, *Stizostedion vitreum*			0.21		0.79		1.00	0.01	<0.01
Yellow perch, *Perca flavescens*		0.29	0.14	0.29	0.29		1.00	<0.01	<0.01
SUNFISHES; CENTRARCHIDAE									
White crappie, *Pomoxis annularis*		0.13			0.88		1.00	0.01	<0.01
DRUMS; SCIAENIDAE									
Freshwater drum, *Aplodinotus grunniens*		0.00	0.22		0.78		1.00	<0.01	<0.01

Table 4.2. Family relative abundance as a fraction of 1.00 in the study segments.

SPECIES	Segment 10	Segment 12	Segment 22
STURGEONS; ACIPENSERIDAE	0.01	0.01	0.02
GARS; LEPISOSTEIDAE			0.01
HERRINGS; CLUPEIDAE			0.43
MOONEYES; HIODONTIDAE	0.16	0.01	0.01
SALMON, TROUT, WHITEFISH; SALMONIDAE		<0.01	
SMELT; OSMERIDAE		<0.01	
PIKES; ESOCIDAE	0.02	<0.01	
CODS; GADIDAE	0.01	<0.01	
MINNOWS; CYPRINIDAE	0.55	0.03	0.27
SUCKERS; CATOSTOMIDAE	0.17	0.94	0.05
BULLHEAD CATFISHES; ICTALURIDAE	0.05	<0.01	0.11
PERCHES; PERCIDAE	0.03	0.01	<0.01
TEMPERATE BASSES; PERCICHTHYIDAE			0.01
SUNFISHES; CENTRARCHIDAE	0.01		0.03
DRUMS; SCIAENIDAE	<0.01		0.07
Total	1.00	1.00	1.00

Table 4.3. Species relative abundance (rel. abun.) as a fraction of 1.00 in segment 12 macrohabitats (CHXO=main channel cross-over, ISB=inside bend, OSB=outside bend, SCC=secondary channel: non-connected, SCN=secondary channel: connected, TRM=tributary mouth).

	MACROHABITAT								
SPECIES	CHXO	ISB	OSB	SCC	SCN	TRM	Total	Combined Rel. Abun. All Macrohabitats	Combined Rel. Abun. CHXO, ISB, OSB
STURGEONS; ACIPENSERIDAE									
Shovelnose sturgeon, *Scaphirhynchus platorynchus*	0.55	0.16	0.18	0.02	0.02	0.06	1.00	0.01	0.24
MOONEYES; HIODONTIDAE									
Goldeye, *Hiodon alosoides*					0.32	0.68	1.00	0.01	
SALMON, TROUT, WHITEFISH; SALMONIDAE									
Ciscoe, *Coregonus artedi*			0.50			0.50	1.00	<0.01	0.01
SMELT; OSMERIDAE									
Rainbow smelt, *Osmerus mordax*	0.07	0.21	0.57	0.14			1.00	<0.01	0.05
PIKES; ESOCIDAE									
Northern pike, *Esox lucius*			0.17		0.67	0.17	1.00	<0.01	
CODS; GADIDAE									
Burbot, *Lota lota*		0.25	0.75				1.00	<0.01	0.02
MINNOWS; CYPRINIDAE									
Common carp, *Cyprinus carpio*			0.17	0.02	0.48	0.33	1.00	0.01	0.05
Emerald shiner, *Notropis atherinoides*						1.00	1.00	<0.01	
Fathead minnow, *Pimephales promelas*		0.09	0.80	0.05	0.03	0.02	1.00	0.01	0.32
Spottail shiner, *Notropis hudsonius*				0.33	0.67		1.00	<0.01	
SUCKERS; CATOSTOMIDAE									
Bigmouth buffalo, *Ictiobus cyprinellus*					1.00		1.00	<0.01	
Blue sucker, *Cycleptus elongatus*						1.00	1.00	<0.01	
Longnose sucker, *Catostomus catostomus*	0.33	0.13	0.47			0.07	1.00	<0.01	0.04
Longnose sucker < 150 mm, *Catostomus catostomus*		<0.01		0.54	0.46		1.00	0.75	0.06
River carpsucker, *Carpiodes carpio*	0.06		0.12	0.05	0.44	0.33	1.00	0.01	0.04
Shorthead redhorse, *Moxostoma macrolepidotum*			0.18		0.35	0.47	1.00	<0.01	0.01
White sucker, *Catostomus commersonii*	0.10	0.13	0.33	0.05	0.39		1.00	<0.01	0.02
White sucker < 150 mm, *Catostomus commersonii*		0.02		0.09	0.89	<0.01	1.00	0.16	0.12

Table 4.3. Continued.

SPECIES	MACROHABITAT						Total	Combined Rel. Abun. All Macrohabitats	Combined Rel. Abun. CHXO, ISB, OSB
	CHXO	ISB	OSB	SCC	SCN	TRM			
BULLHEAD CATFISHES; ICTALURIDAE									
Channel catfish, *Ictalurus punctatus*					0.48	0.52	1.00	<0.01	
PERCHES; PERCIDAE									
Johnny darter, *Etheostoma nigrum*					1.00		1.00	<0.01	
Sauger, *Stizostedion canadense*					0.20	0.80	1.00	<0.01	
Walleye, *Stizostedion vitreum*		0.03	0.09		0.13	0.75	1.00	<0.01	0.02
Yellow perch, *Perca flavescens*					0.83	0.17	1.00	<0.01	

Table 4.4. Species relative abundance (rel. abun.) as a fraction of 1.00 in segment 22 macrohabitats (CHXO=main channel cross-over, ISB=inside bend, OSB=outside bend, SCC=secondary channel: non-connected, SCN=secondary channel: connected, TRM=tributary mouth).

MACROHABITAT

SPECIES	CHXO	ISB	OSB	SCC	SCN	TRM	Total	Combined Rel. Abun. All Macrohabitats	Combined Rel. Abun. CHXO, ISB, OSB
STURGEONS; ACIPENSERIDAE									
Shovelnose sturgeon, *Scaphirhynchus platorynchus*		1.00					1.00	0.02	0.04
GARS; LEPISOSTEIDAE									
Longnose gar, *Lepisosteus osseus*		0.19				0.81	1.00	<0.01	<0.01
Shortnose gar, *Lepisosteus platostomus*		0.18			0.17	0.65	1.00	0.01	<0.01
HERRINGS; CLUPEIDAE									
Gizzard shad, *Dorosoma cepedianum*		0.13	0.03	<0.01	0.11	0.72	1.00	0.43	0.23
MOONEYES; HIODONTIDAE									
Goldeye, *Hiodon alosoides*		0.03	0.05	0.06	0.04	0.81	1.00	0.01	<0.01
MINNOWS; CYPRINIDAE									
Creek chub, *Semotilus atromaculatus*		1.00					1.00	<0.01	<0.01
Common carp, *Cyprinus carpio*		0.15	0.21		0.10	0.54	1.00	0.02	0.02
Common carp < 150mm, *Cyprinus carpio*		0.07	0.71			0.21	1.00	<0.01	<0.01
Emerald shiner, *Notropis atherinoides*		0.43	0.44	0.07	0.01	0.06	1.00	0.13	0.28
Fathead minnow, *Pimephales promelas*		0.67				0.33	1.00	<0.01	<0.01
Flathead chub, *Platygobio gracilis*		0.75	0.25				1.00	<0.01	<0.01
Goldfish, *Carassius auratus*		1.00					1.00	<0.01	<0.01
Grass carp, *Ctenopharyngodon idellus*							1.00	<0.01	<0.01
Hybognathus spp.		0.49	0.10	<0.01	0.34	0.07	1.00	0.08	0.08
Red shiner, *Cyprinella lutrensis*		0.08	0.30		0.01	0.60	1.00	0.01	0.02
River shiner, *Notropis blennius*		0.60	0.24	0.02		0.14	1.00	0.01	0.02
Sand shiner, *Notropis ludibundus*		0.29	0.45			0.27	1.00	<0.01	<0.01
Sicklefin chub, *Macrhybopsis meeki*		0.83				0.17	1.00	<0.01	<0.01
Silver chub, *Macrhybopsis storeriana*		0.52	0.13		0.13	0.22	1.00	0.01	0.01
Sturgeon chub, *Macrhybopsis gelida*	0.07	0.46	0.39			0.07	1.00	<0.01	<0.01
SUCKERS; CATOSTOMIDAE									
Bigmouth buffalo, *Ictiobus cyprinellus*						1.00	1.00	<0.01	
Blue sucker, *Cycleptus elongatus*		0.72	0.28				1.00	<0.01	0.01
Golden redhorse, *Moxostoma erythrurum*						1.00	1.00	<0.01	

Table 4.4. Continued.

MACROHABITAT

SPECIES	CHXO	ISB	OSB	SCC	SCN	TRM	Total	Combined Rel. Abun. All Macrohabitats	Combined Rel. Abun. CHXO, ISB, OSB
SUCKERS; CATOSTOMIDAE									
Highfin carpsucker, *Carpiodes velifer*						1.00	1.00	<0.01	
Quillback, *Carpiodes cyprinus*		0.50	0.07			0.43	1.00	<0.01	<0.01
River carpsucker, *Carpiodes carpio*		0.18			0.23	0.59	1.00	0.02	<0.01
River carpsucker <150 mm, *Carpiodes carpio*		0.37	0.04		0.20	0.40	1.00	0.01	0.01
River redhorse, *Moxostoma carinatum*					1.00		1.00	<0.01	
Smallmouth buffalo, *Ictobius bubalus*		0.25				0.75	1.00	<0.01	<0.01
BULLHEAD CATFISHES; ICTALURIDAE									
Blue catfish, *Ictalurus furcatus*	0.01	0.51				0.48	1.00	0.01	0.01
Channel catfish, *Ictalurus punctatus*	<0.01	0.52	0.26		0.03	0.18	1.00	0.07	0.14
Flathead catfish, *Pylodictis olivaris*		0.09	0.86		0.01	0.04	1.00	0.02	0.04
Slender madtom, *Noturus exilis*		1.00					1.00	<0.01	<0.01
Stonecat, *Noturus flavus*		0.50	0.38			0.13	1.00	<0.01	<0.01
PERCHES; PERCIDAE									
Sauger, *Stizostedion canadense*		0.03	0.21		0.18	0.58	1.00	<0.01	<0.01
Walleye, *Stizostedion vitreum*						1.00	1.00	<0.01	
TEMPERATE BASSES; PERCICHTHYIDAE									
White bass, *Morone chrysops*		0.41	0.09		0.11	0.39	1.00	0.01	<0.01
SUNFISHES; CENTRARCHIDAE									
Black crappie, *Pomoxis nigromaculatus*					0.40	0.60	1.00	<0.01	
Bluegill, *Lepomis macrochirus*		0.04	0.07		0.18	0.71	1.00	0.01	
Green sunfish, *Lepomis cyanellus*		0.02	0.58		0.01	0.39	1.00	0.01	0.01
Largemouth bass, *Micropterus salmoides*		0.02	0.14		0.25	0.59	1.00	<0.01	<0.01
Orangespotted sunfish, *Lepomis humilis*		0.22	0.03		0.32	0.42	1.00	0.01	<0.01
White crappie, *Pomoxis annularis*		0.50			0.19	0.31	1.00	<0.01	<0.01
DRUMS; SCIAENIDAE									
Freshwater drum, *Aplodinotus grunniens*		0.19	0.26		0.03	0.52	1.00	0.07	0.04

Table 4.5. Species diversity measures for the three study segments (rarefaction estimate based on a sample of 1000 individuals).

Species Diversity Measures	Segment		
	10	12	22
Heterogeneity			
Reciprocal of Simpson's index (1/D, equation *4.2*)	6.88	1.67	5.69
Richness			
Rarefaction method	28.46	15.72	31.72
Evenness			
Smith and Wilson's index (E, equation *4.3*)	0.23	0.17	0.16

Table 4.6. Fineness ratio and physiochemical characterization (mean, range, coefficient of variation (CV)) for segment 10 macrohabitats. (CHXO=main channel cross-over, ISB=inside bend, OSB=outside bend, SCC=secondary channel: connected, SCN=secondary channel: non-connected, TRM=tributary mouth).

Variable	Macrohabitat					
	CHXO	ISB	OSB	SCC	SCN	TRM
Fineness Ratio	5.54	4.60	4.93	4.29	3.55	4.75
Range	3.00-7.85	2.75-7.85	3.00-7.85	2.90-7.85	2.75-7.83	2.90-7.85
CV	0.14	0.14	0.14	0.08	0.08	0.00
Mean Depth (m)	4.55	2.76	3.51	0.83	1.07	3.64
Range	3.3-6.73	0.55-4.23	2.16-5.63	0.19-3.36	0.67-1.78	3.34-3.94
CV	0.25	0.59	0.29	1.27	0.31	0.00
Mean Current Velocity (m/sec)	1.12	0.84	0.73	0.26	0.01	0.64
Range	0.92-1.38	0.15-1.3	0.60-0.89	0.08-0.78	0.00-0.05	0.61-0.68
CV	0.15	0.55	0.15	1.04	0.71	0.00
Geometric Mean of Substrate (mm)	1.56	0.96	1.94	0.60	0.04	0.83
Range	1.03-5.31	0.11-1.30	0.78-8.44	0.14-0.98	0.03-0.05	0.80-0.86
CV	0.94	1.31	1.69	0.73	0.08	0.00

Table 4.7. Fineness ratio and physiochemical characterization (mean, range, coefficient of variation (CV)) for segment 12 macrohabitats. (CHXO=main channel cross-over, ISB=inside bend, OSB=outside bend, SCC=secondary channel: connected, SCN=secondary channel: non-connected, TRM=tributary mouth).

Variable	Macrohabitat					
	CHXO	ISB	OSB	SCC	SCN	TRM
Fineness Ratio	5.85	5.39	4.49	4.89	4.00	4.08
Range	2.86-7.84	4.50-7.84	2.86-7.84	2.86-7.84	2.86-7.84	2.86-7.84
CV	0.13	0.26	0.29	0.03	0.25	0.06
Mean Depth (m)	3.08	1.74	3.19	0.55	1.21	2.27
Range	1.69-4.53	0.27-3.27	1.95-4.91	0.12-2.72	0.42-1.79	1.64-2.86
CV	0.21	0.75	0.16	1.00	0.27	0.10
Mean Current Velocity (m/sec)	1.05	0.68	0.84	0.15	0.01	0.04
Range	0.84-1.60	0.16-1.60	0.59-1.38	0.03-0.23	0.00-0.04	0.00-0.09
CV	0.21	0.69	0.18	0.95	0.00	1.02
Geometric Mean of Substrate (mm)	5.59	1.42	11.21	0.67	0.06	0.07
Range	1.03-25.54	1.01-3.43	0.86-34.55	0.03-1.03	0.03-0.11	0.03-0.12
CV	1.75	0.41	1.18	0.51	0.51	0.77

Table 4.8. Fineness ratio and physiochemical characterization (mean, range, coefficient of variation (CV)) for segment 22 macrohabitats. (CHXO=main channel cross-over, ISB=inside bend, OSB=outside bend, SCC=secondary channel: connected, SCN=secondary channel: non-connected, TRM=tributary mouth).

Variable	Macrohabitat					
	CHXO	ISB	OSB	SCC	SCN	TRM
Fineness Ratio	4.51	4.99	4.12	3.93	3.75	3.94
Range	2.97-5.63	2.14-10.44	2.14-6.36	-	2.14-9.69	2.90-10.44
CV	0.21	0.33	0.22	-	0.50	0.50
Mean Depth (m)	6.08	2.19	1.32	0.48	0.75	1.29
Range	4.50-7.50	1.65-5.94	3.47-5.60	-	0.70-0.87	0.56-3.66
CV	0.21	0.82	1.12	-	0.26	0.81
Mean Current Velocity (m/sec)	1.67	0.38	0.46	0.34	0.07	0.07
Range	1.30-1.83	0.25-0.80	1.01-1.44	-	0.00-0.16	0.00-0.27
CV	0.14	0.84	0.72	-	1.45	3.07
Geometric Mean of Substrate (mm)	1.12	9.93	28.83	0.09	0.03	0.24
Range	1.03-1.24	8.80-13.09	1.04-52.10	-	0.03-0.03	0.03-1.53
CV	0.06	0.30	0.43	-	0.00	2.03

Table 4.9. Results of ANOVA and multiple comparison testing of segment fineness ratio and physiochemical variables measured in main channel cross-over (CHXO), inside bend (ISB), and outside bend (OSB) macrohabitats.

Physiochemical Variable	Macrohabitat	Results of omnibus ****ANOVA p-value	x_r^2	***Results of multiple comparison testing Segment 10	12	22
Mean Depth (m)	**CHXO	<u>≤0.0001</u>	40.05	12,22	10,22	10,12
	*ISB	**0.0403**	7.10		22	12
	**OSB	<u>0.0005</u>	35.47	22	22	10,12
Mean Current Velocity (m/sec)	**CHXO	<u>≤0.0001</u>	39.86	22	22	10,12
	ISB	0.2141	4.60	~	~	~
	**OSB	<u>0.0005</u>	35.46	22	22	10,12
Geometric Mean of Substrate	CHXO	0.7209	1.90	~	~	~
	*ISB	<u>0.0005</u>	39.80	22	22	10,12
	**OSB	<u>≤0.0001</u>	41.07	22	22	10,12
Mean Fineness Ratio	**CHXO	**0.0428**	7.01	22		10
	ISB	0.4790	2.70	~	~	~
	OSB	0.5606	2.55	~	~	~

*Tukey-type multiple comparison test was performed on ranks.
**Tukey-type multiple comparison test for unequal sample sizes was performed on ranks.
***a segment is significantly different from segments whose number is below it.
****Friedman's Analysis of Variance performed on ranks.
~multiple comparison test was not performed.
probabilities in **bold** are significant at the 0.05 level ($P < 0.05$)
probabilities that are <u>underlined</u> are significant at the 0.01 level ($P < 0.01$)

Table 4.10. Results of ANOVA testing of segment fineness ratio and physiochemical variable variation measured in main channel cross-over (CHXO), inside bend (ISB), and outside bend (OSB) macrohabitats (*Friedman's analysis of variance performed on ranks; CV=coefficient of variation).

Physiochemical Variable	Macrohabitat	x_r^2	Results of omnibus *ANOVA p-value
Depth (m) CV	CHXO	4.51	0.2635
	ISB	5.27	0.1634
	OSB	2.81	0.4185
Current Velocity (m/sec) CV	CHXO	1.85	0.7949
	ISB	5.19	0.1332
	OSB	2.01	0.6696
Geometric Mean of Substrate CV	CHXO	1.97	0.6967
	ISB	2.79	0.4181
	OSB	4.21	0.3749
Fineness Ratio CV	CHXO	4.60	0.2750
	ISB	4.47	0.2257
	OSB	1.50	0.8047

Probabilities in **bold** are significant at the 0.05 level ($P<0.05$)
Probabilities that are underlined are significant at the 0.01 level ($P<0.01$)

Table 4.11. Relationship between fineness ratio coefficient of variation (CV) and physiochemical variable CV in macrohabitats.

Physiochemical Variable	Segment		
	10	12	22
Current Velocity (m/s)			
R	0.59	0.59	0.81
R^2	0.35	0.34	0.66
P-value	**0.0391**	**0.0450**	<u>0.0044</u>
Depth (m)			
R	0.13	0.44	0.33
R^2	0.02	0.19	0.11
P-value	0.6801	0.1517	0.3473
Substrate Geometric Mean			
R	0.61	0.65	0.85
R^2	0.37	0.42	0.72
P-value	**0.0350**	**0.0235**	<u>0.0020</u>

Probabilities in **bold** are significant at the 0.05 level ($P < 0.05$)
Probabilities that are <u>underlined</u> are significant at the 0.01 level (P<0.01)

Table 4.12. Fineness ratios, mean current velocity (m/sec), and maximum current velocity for species in segment 10.

SPECIES	Fineness Ratio	Mean Current Velocity	Maximum Current Velocity
STURGEONS; ACIPENSERIDAE			
Shovelnose sturgeon	8.60	0.88	1.15
MOONEYES; HIODONTIDAE			
Goldeye	3.60	0.16	1.10
PIKES; ESOCIDAE			
Northern pike	6.22	0.06	0.30
CODS; GADIDAE			
Burbot	7.83	0.25	0.50
MINNOWS; CYPRINIDAE			
Common carp	3.19	0.15	1.30
Common carp < 150 mm	2.91	0.05	0.27
Emerald shiner	5.04	0.19	0.50
Flathead chub	4.57	0.17	1.05
Sicklefin chub	5.24	0.97	1.30
Spottail shiner	4.46	0.24	1.00
Sturgeon chub	5.45	0.88	1.25
Western silvery minnow	4.23	0.14	0.85
SUCKERS; CATOSTOMIDAE			
Bigmouth buffalo	3.01	0.02	0.25
River carpsucker	2.70	0.06	1.00
River carpsucker < 150 mm	3.27	0.03	0.17
Shorthead redhorse	4.05	0.09	0.35
Smallmouth buffalo	2.80	0.06	0.90
Smallmouth buffalo < 150 mm	3.10	0.05	0.27
BULLHEAD CATFISHES; ICTALURIDAE			
Channel catfish	4.86	0.42	1.35
Stonecat	5.78	0.62	1.25
PERCHES; PERCIDAE			
Sauger	5.98	0.16	0.50
Walleye	4.92	0.05	0.35
Yellow perch	3.97	0.10	0.27

Table 4.12. Continued.

SPECIES	Fineness Ratio	Average Current Velocity	Maximum Current Velocity
SUNFISHES; CENTRARCHIDAE			
White crappie	2.75	0.08	0.17
DRUMS; SCIAENIDAE			
Freshwater drum	3.02	0.07	0.30

Table 4.13. Fineness ratios, mean current velocity (m/sec), and maximum current velocity for species in segment 12.

SPECIES	Fineness Ratio	Mean Current Velocity	Maximum Current Velocity
STURGEONS; ACIPENSERIDAE			
Shovelnose sturgeon	8.58	0.77	1.15
MOONEYES; HIODONTIDAE			
Goldeye	3.60	0.09	0.15
SALMON, TROUT, WHITEFISH; SALMONIDAE			
Cisco	3.68	0.25	0.50
SMELT; OSMERIDAE			
Rainbow smelt	6.50	0.60	1.20
PIKES; ESOCIDAE			
Northern pike	5.81	0.02	0.10
CODS; GADIDAE			
Burbot	7.80	0.46	0.75
MINNOWS; CYPRINIDAE			
Common carp	3.37	0.03	0.35
Emerald shiner	5.12	0.00	0.00
Fathead minnow	4.51	0.10	0.35
Spottail shiner	4.34	0.01	0.03
SUCKERS; CATOSTOMIDAE			
Bigmouth buffalo	3.03	0.02	0.10
Blue sucker	4.41	0.07	0.07
Longnose sucker	4.63	1.00	1.45
Longnose sucker < 150 mm	4.95	0.07	0.37
River carpsucker	2.86	0.08	0.85
Shorthead redhorse	3.70	0.12	0.45
White sucker	4.47	0.27	1.65
White sucker < 150 mm	4.63	0.04	0.40
BULLHEAD CATFISHES; ICTALURIDAE			
Channel catfish	4.87	0.07	0.15
PERCHES; PERCIDAE			
Johnny darter	5.69	0.00	0.00
Sauger	6.12	0.02	0.10
Walleye	4.96	0.13	0.90
Yellow perch	3.93	0.01	0.05

Table 4.14. Fineness ratios, mean current velocity (m/sec), and maximum current velocity for species in segment 22.

SPECIES	Fineness Ratio	Mean Current Velocity	Maximum Current Velocity
STURGEONS; ACIPENSERIDAE			
Shovelnose sturgeon	**8.58**	0.42	0.90
GARS; LEPISOSTEIDAE			
Longnose gar	*10.44*	0.08	0.40
Shortnose gar	9.69	0.03	0.60
HERRINGS; CLUPEIDAE			
Gizzard shad	2.88	0.16	1.55
MOONEYES; HIODONTIDAE			
Goldeye	3.54	0.11	0.70
MINNOWS; CYPRINIDAE			
Creek chub	4.62	0.18	0.35
Common carp	**3.37**	0.14	1.55
Common carp < 150 mm	2.91	0.03	0.60
Emerald shiner	4.81	0.30	1.70
Fathead minnow	4.14	0.11	0.30
Flathead chub	**4.57**	0.46	1.30
Goldfish	*2.30*	0.07	0.10
Grass carp	3.75	0.30	0.30
Hybognathus spp.	**4.41**	0.23	0.90
Red shiner	3.35	0.17	0.55
River shiner	4.62	0.22	0.85
Sand shiner	4.49	0.24	0.45
Sicklefin chub	**5.24**	0.57	0.75
Silver chub	**4.36**	0.18	1.40
Sturgeon chub	**5.63**	1.00	1.95
SUCKERS; CATOSTOMIDAE			
Bigmouth buffalo	**3.00**	0.00	0.00
Blue sucker	**4.57**	0.72	1.70
Golden redhorse	*3.50*	0.03	0.05
Highfin carpsucker	*2.74*	0.05	0.05
Quillback	*2.78*	0.07	0.35
River carpsucker	**2.80**	0.04	0.40
River carpsucker < 150 mm	3.20	0.13	0.65
River redhorse	*3.96*	0.30	0.30

Table 4.14. Continued.

SPECIES	Fineness Ratio	Average Current Velocity	Maximum Current Velocity
SUCKERS; CATOSTOMIDAE			
Smallmouth buffalo	**2.90**	0.14	0.45
BULLHEAD CATFISHES; ICTALURIDAE			
Blue catfish	<u>3.91</u>	0.42	1.50
Channel catfish	<u>4.84</u>	0.39	2.10
Flathead catfish	*4.67*	0.36	0.85
Slender madtom	*6.36*	0.45	0.45
Stonecat	<u>5.67</u>	0.59	1.40
PERCHES; PERCIDAE			
Sauger	**6.12**	0.12	0.85
Walleye	**4.90**	0.00	0.00
TEMPERATE BASSES; PERCICHTHYIDAE			
White bass	<u>2.14</u>	0.13	0.85
SUNFISHES; CENTRARCHIDAE			
Black crappie	*2.34*	0.01	0.08
Bluegill	<u>2.15</u>	0.05	0.45
Green sunfish	<u>2.51</u>	0.16	0.45
Largemouth bass	*3.18*	0.05	0.35
Orangespotted sunfish	<u>2.40</u>	0.10	0.45
White crappie	<u>2.63</u>	0.02	0.20
DRUMS; SCIAENIDAE			
Freshwater drum	<u>2.97</u>	0.23	1.60

<u>FR</u> computed from specimens housed in Sternberg Museum of Natural History, Fort Hays State University, Hays, Kansas
FR computed from specimens collected from other Missouri River segments
FR obtained from the literature

Table 5.1. Physiochemical characterization (mean, range, standard deviation (SD), coefficient of variation (CV)) of segment 5 macrohabitats (CHXO=main channel cross-over, ISB=inside bend, OSB=outside bend, SCC=secondary channel: connected, SCN= secondary channel: non-connected, TRM=tributary mouth).

Variable	Macrohabitat					
	CHXO	ISB	OSB	SCC	SCN	TRM
Mean Depth (m)	2.3	1.3	1.9	1.2	0.6	-
Range	1.4-4.1	0.9-2.3	1.1-3.4	0.3-4.2	0.3-0.9	
SD	0.81	0.37	0.75	1.16	0.20	
CV	35.4	29.7	39.3	100.4	32.3	
Mean Current Velocity (m/sec)	0.72	0.58	0.70	0.38	0.00	-
Range	0.28-1.02	0.36-0.82	0.30-0.96	0.11-0.72	0.00-0.00	
SD	0.23	0.13	0.20	0.17	0.00	
CV	31.6	23.1	29.3	44.1	0.0	
Mean Temperature (Celsius)	21.7	21.4	21.6	22.5	22.5	-
Range	16.0-24.7	15.9-25.7	16.0-24.2	15.8-27.2	18.4-26.9	
SD	1.98	2.39	2.02	2.89	3.60	
CV	9.1	11.1	9.3	12.9	16.0	
Turbidity (NTU)	23.6	42.4	37.4	21.0	43.0	-
Range	10.8-88.5	15.2-159.7	25.4-37.4	11.5-43.0	22.6-70.8	
SD	19.47	39.62	39.68	8.79	20.58	
CV	82.5	93.4	106.1	41.9	47.9	
Geometric Mean of Substrate (mm)	11.17	4.90	10.46	2.47	0.08	-
Range	1.03-52.26	0.60-17.62	0.22-36.21	0.06-6.62	0.03-0.26	
SD	16.00	4.42	10.83	2.43	0.09	
CV	143.2	90.2	103.5	98.4	0.2	

Table 5.2. Physiochemical characterization (mean, range, standard deviation (SD), coefficient of variation (CV)) of segment 8 macrohabitats (CHXO=main channel cross-over, ISB=inside bend, OSB=outside bend, SCC=secondary channel: connected, SCN= secondary channel: non-connected, TRM=tributary mouth).

Variable	Macrohabitat					
	CHXO	ISB	OSB	SCC	SCN	TRM
Mean Depth (m)	3.0	1.6	3.9	1.4	1.4	2.1
Range	1.5-5.0	1.2-2.8	1.9-7.1	0.4-3.1	0.8-3.0	0.9-3.4
SD	0.97	0.41	1.34	0.86	0.55	0.83
CV	29.8	26.4	34.4	63.2	39.9	39.8
Mean Current Velocity (m/sec)	0.81	0.56	0.84	0.45	0.03	0.60
Range	0.50-1.03	0.36-0.92	0.43-1.20	0.12-1.03	0.00-0.18	0.00-0.53
SD	0.15	0.14	0.20	0.23	0.06	0.15
CV	18.9	25.5	24.0	51.9	212.7	212.7
Mean Temperature (Celsius)	17.5	17.2	17.5	18.9	19.4	17.3
Range	11.2-21.7	11.9-22.0	11.5-22.7	11.9-23.5	11.2-26.8	9.8-22.4
SD	2.94	3.09	2.81	3.67	3.85	3.83
CV	16.8	17.9	16.1	19.4	19.8	19.8
Turbidity (NTU)	91.0	90.4	89.8	65.4	64.0	49.8
Range	19.5-382.8	33.7-329.8	21.8-341.7	35.2-97.4	23.4-263.0	16.0-202.5
SD	98.76	95.08	91.88	18.37	59.33	53.05
CV	108.5	105.2	102.3	28.1	92.1	92.1
Geometric Mean of Substrate (mm)	1.52	0.87	3.55	0.76	0.21	0.11
Range	0.76-7.55	0.60-1.14	0.70-30.31	0.23-1.23	0.03-1.19	0.03-0.81
SD	1.68	0.19	7.51	0.34	0.33	0.22
CV	110.8	21.4	211.3	44.6	157.9	157.9

Table 5.3. Physiochemical characterization (mean, range, standard deviation (SD), coefficient of variation (CV)) of segment 9 macrohabitats (CHXO=main channel cross-over, ISB=inside bend, OSB=outside bend, SCC=secondary channel: connected, SCN= secondary channel: non-connected, TRM=tributary mouth).

Variable	Macrohabitat					
	CHXO	ISB	OSB	SCC	SCN	TRM
Mean Depth (m)	2.4	1.6	3.4	0.9	1.1	1.2
Range	1.2-3.9	0.3-3.6	1.6-3.7	0.3-2.2	0.7-1.5	0.7-1.8
SD	0.69	0.75	1.52	0.74	0.26	0.55
CV	35.4	47.9	45.2	78.7	23.8	44.7
Mean Current Velocity (m/sec)	0.90	0.48	0.88	0.41	0.02	0.00
Range	0.33-1.62	0.05-0.96	0.28-1.62	0.12-1.01	0.00-0.12	0.00-0.00
SD	0.43	0.21	0.36	0.29	0.04	0.00
CV	47.3	44.1	40.8	71.1	198.2	0.0
Mean Temperature (Celsius)	22.6	22.7	22.4	22.6	21.9	23.1
Range	16.1-25.3	16.4-25.9	15.9-25.1	17.5-25.9	15.5-26.3	21.4-24.2
SD	2.70	2.63	2.80	3.07	3.22	1.48
CV	12.0	11.6	12.5	13.6	14.7	6.4
Turbidity (NTU)	183.1	168.1	157.3	122.9	102.4	282.6
Range	16.6-744.7	23.0-798.3	16.2-707.7	16.7-819.3	13.0-827.6	32.3-648.0
SD	260.31	238.41	224.12	225.79	203.49	323.61
CV	142.2	141.2	142.5	183.7	198.8	114.5
Geometric Mean of Substrate (mm)	11.12	7.07	15.93	8.72	0.23	0.04
Range	0.95-29.50	0.23-17.36	0.96-101.60	0.53-25.44	0.03-1.31	0.03-0.54
SD	10.44	6.74	24.14	8.38	0.41	0.01
CV	93.9	95.3	151.5	96.1	175.0	30.3

Table 5.4. Physiochemical characterization (mean, range, standard deviation (SD), coefficient of variation (CV)) of segment 10 macrohabitats (CHXO=main channel cross-over, ISB=inside bend, OSB=outside bend, SCC=secondary channel: connected, SCN= secondary channel: non-connected, TRM=tributary mouth).

Variable	Macrohabitat					
	CHXO	ISB	OSB	SCC	SCN	TRM
Mean Depth (m)	5.3	2.5	3.9	1.0	1.2	3.6
Range	3.3-10.3	0.4-5.4	2.2-5.6	0.2-4.2	0.6-2.4	3.34-3.94
SD	1.89	1.77	1.08	1.29	0.58	0.42
CV	29.2	71.1	27.7	132.9	48.8	
Mean Current Velocity (m/sec)	1.03	0.71	0.70	0.27	0.01	0.65
Range	0.54-1.38	0.13-1.30	0.58-0.89	0.08-0.78	0.00-0.05	0.61-0.68
SD	0.23	0.46	0.10	0.25	0.02	0.05
CV	22.2	64.5	13.6	90.9	316.2	
Mean Temperature (Celsius)	20.6	21.0	20.5	20.5	21.0	21.9
Range	18.2-23.9	18.4-23.9	16.7-24.3	15.5-24.3	15.6-24.2	20.1-23.6
SD	2.14	2.04	2.74	2.54	3.07	2.51
CV	10.4	9.7	13.3	12.4	14.7	
Turbidity (NTU)	349.8	278.6	162.7	122.0	65.1	216.2
Range	57.9-999.9	53.1-999.9	60.7-367.0	50.6-320.7	24.8-125.8	197.1-235.3
SD	358.19	311.43	107.60	75.52	31.02	27.03
CV	102.4	111.8	66.1	61.9	47.7	
Geometric Mean of Substrate (mm)	1.37	0.85	4.32	0.80	0.06	0.83
Range	0.83-5.31	0.11-1.56	0.78-34.55	0.14-3.22	0.03-0.24	0.80-0.86
SD	1.10	0.48	9.32	0.78	0.07	0.04
CV	80.4	56.9	97.5	97.5	110.4	

Table 5.5. Daily river discharge (m^3/sec) averaged for the three year study period (1996, 1997, and 1998; Three month=July, August, and September).

	Segment			
	5	**8**	**9**	**10**
Twelve month				
Mean	318.7	375.7	438.1	813.8
Range	1258.1	624.4	2347.5	2541.2
Coefficient of variation	65.7	30.1	86.5	43.9
Three month				
Mean	294.8	397.5	459.0	856.5
Range	679.3	382.0	1468.2	1485.2
Coefficient of variation	53.4	27.0	65.0	30.8

Table 5.6. Results of macrohabitat x segment canonical analysis of variates and ANOVA performed on macrohabitat physiochemical variables. Relative %=relative contribution to total dispersion.

Physiochemical Variable	Standardized Coefficients for Canonical Variable I	Standardized Coefficients for Canonical Variable II	Standardized Coefficients for Canonical Variable III	Probability Value for ANOVA F-test
Depth (m)	1.2512	0.2641	-0.4200	0.0001
Current Velocity (m/s)	0.5102	0.0859	0.0488	0.0037
Temperature (Celsius)	-0.2534	0.3541	-0.4740	0.3483
Turbidity (NTU)	0.3316	0.2109	0.2509	0.1878
%Sand	0.0924	0.5580	1.5696	0.0153
%Silt	0.9586	-1.1201	1.3341	0.0040
Eigenvalues	0.4022	0.103	0.0795	
Relative %	59	15	12	

Table 5.7. Species relative abundance as a fraction of 1.00 in study segments (CHXO=main channel cross-over ISB=inside bend, OSB=outside bend, SCC=secondary channel: connected, SCN=secondary non:connected, TRM=tributary mouth).

MACROHABITAT

Species	CHXO	ISB	OSB	SCC	SCN	TRM
Segment 5						
Flathead chub	0.01	0.55	0.21	0.22	0.01	-
Sicklefin chub	0.27	0.31	0.16	0.25	0.00	-
Sturgeon chub	0.23	0.25	0.25	0.27	0.00	-
Segment 8						
Flathead chub	0.01	0.51	0.02	0.36	0.09	0.01
Sicklefin chub	0.38	0.23	0.19	0.15	0.00	0.05
Sturgeon chub	0.09	0.22	0.18	0.25	0.00	0.27
Segment 9						
Flathead chub	0.00	0.32	0.01	0.35	0.32	0.00
Sicklefin chub	0.30	0.36	0.08	0.25	0.00	0.00
Sturgeon chub	0.25	0.40	0.12	0.22	0.01	0.00
Segment 10						
Flathead chub	0.00	0.40	0.06	0.51	0.00	0.03
Sicklefin chub	0.33	0.17	0.39	0.09	0.00	0.02
Sturgeon chub	0.11	0.48	0.24	0.16	0.00	0.00

Table 5.8. Physiochemical characterization (mean, range, coefficient of variation (CV)) of flathead chub capture sites.

Variable	Segment			
	5	8	9	10
Depth (m)	1.3	1.0	0.9	0.8
Range	0.1-4.8	0.1-4.0	0.2-4.6	0.1-3.8
CV	0.27	0.90	0.80	0.66
Current Velocity (m/sec)	0.50	0.35	0.28	0.21
Range	0.00-1.05	0.00-1.20	0.00-1.55	0.00-1.05
CV	0.93	0.23	0.28	0.19
Temperature (Celsius)	20.4	17.9	22.0	20.7
Range	14.2-26.8	11.2-27.8	12.1-30.0	15.3-25.3
CV	3.56	2.55	2.91	1.99
Turbidity (NTU)	36.7	80.9	146.2	161.2
Range	7.4-305.0	17.2-479.0	10.0-999.9	38.0-999.9
CV	49.95	54.28	211.74	146.45
Geometric Mean of Substrate (mm)	5.03	0.70	6.46	0.99
Range	0.03-33.00	0.03-1.45	0.03-33.00	0.03-11.66
CV	7.80	0.40	8.85	1.85
% Silt	29.8	23.7	33.1	31.6
% Sand	41.7	75.8	40.2	58.5
% Gravel	28.6	0.5	26.7	10.0

Table 5.9. Physiochemical characterization (mean, range, coefficient of variation (CV)) of sicklefin chub capture sites.

Variable	Segment			
	5	8	9	10
Depth (m)	2.0	3.0	2.4	4.7
Range	0.8-4.4	1.1-4.7	0.5-5.5	2.3-10.6
CV	0.69	0.98	0.66	1.49
Current Velocity (m/sec)	0.77	0.80	0.71	0.93
Range	0.20-1.25	0.25-1.10	0.07-1.55	0.55-1.30
CV	0.23	0.18	0.24	0.14
Temperature (Celsius)	20.7	17.8	21.8	20.7
Range	14.2-24.7	13.5-22.0	15.0-25.5	18.1-25.0
CV	2.38	1.33	2.54	0.66
Turbidity (NTU)	26.6	62.6	172.4	187.7
Range	2.2-166.0	17.2-436.0	16.0-999.9	56.5-939.0
CV	14.93	43.03	215.50	117.89
Geometric Mean of Substrate (mm)	5.69	1.09	7.04	1.30
Range	0.03-33.00	0.36-2.45	0.60-33.00	0.73-5.83
CV	6.98	0.24	10.69	0.57
% Silt	9.6	1.1	1.6	0.9
% Sand	61.3	97.0	66.6	94.0
% Gravel	29.1	2.0	31.8	5.1

Table 5.10. Physiochemical characterization (mean, range, coefficient of variation (CV)) of sturgeon chub capture sites.

Variable	Segment			
	5	8	9	10
Depth (m)	1.9	2.6	2.0	3.2
Range	0.2-5.4	0.5-6.1	0.2-6.8	0.2-7.6
CV	0.78	1.00	1.22	1.73
Current Velocity (m/sec)	0.75	0.76	0.68	0.75
Range	0.20-1.25	0.17-1.45	0.00-2.00	0.10-1.25
CV	0.25	0.26	0.44	0.34
Temperature (Celsius)	20.6	18.2	21.8	20.2
Range	14.2-25.6	11.9-22.9	15.0-30.0	18.3-23.9
CV	2.80		2.82	1.67
Turbidity (NTU)	26.3	85.1	156.9	303.6
Range	2.2-166.0	13.8-543.0	15.6-999.9	53.6-999.9
CV	14.70	73.47	201.96	228.64
Geometric Mean of Substrate (mm)	5.62	1.64	8.14	2.17
Range	0.03-33.00	0.03-33.00	0.03-33.00	0.730-23.70
CV	7.24	2.73	10.48	3.23
% Silt	9.5	11.1	8.3	9.1
% Sand	62.3	85.2	55.0	81.1
% Gravel	28.2	3.8	36.7	9.8

Table 5.11. Results of maximum-likelihood analysis of variance performed on species presence (1) / absence (0) counts in macrohabitat replicates.

| Species | Probability Values | | | |
	Year	Segment	Macrohabitat	Segment x Macrohabitat
Flathead chub	**0.0015**	**0.0074**	**<0.0001**	**0.0038**
Sicklefin chub	**0.0156**	**0.0341**	**<0.0001**	0.2448
Sturgeon chub	0.8113	**<0.0001**	**0.0005**	0.6051

Probabilities in **bold** are significant at the 0.05 level ($P < 0.05$).

Table 5.12. Differences in flathead chub macrohabitat use among segments using simple-effects contrasts.

Macrohabitat	Probability values
Main channel cross-over	0.2584
Inside bend	**0.0116**
Outside bend	**0.0037**
Secondary channel: connected	0.7964
Secondary channel: non-connected	**0.0092**

Probabilities in **bold** are significant at the 0.05 level ($P<0.05$).

Table 5.13. Results of species x segment canonical analysis of variates and ANOVA performed on habitat use data. Relative %=relative contribution to total dispersion.

Physiochemical Variable	Standardized Coefficients for Canonical Variable I	Standardized Coefficients for Canonical Variable II	Probability Value for ANOVA F-test
Depth (m)	1.0697	0.0631	<0.0001
Current Velocity (m/s)	0.3770	-0.1990	<0.0001
Temperature (Celsius)	-0.0065	-0.0278	0.5877
Turbidity (NTU)	0.0213	1.1115	0.0166
%Sand	0.0009	0.3298	0.3849
%Silt	0.3085	-0.2246	0.5907
Eigenvalues	0.1088	0.0114	
Relative %	88	9	

Table 5.14. Pairwise comparison of species habitat use within segments using Hotelling's T^2 (FH=flathead chub, SF=sicklefin chub, SG=sturgeon chub).

Comparison	Segment							
	5	T^2 value	8	T^2 value	9	T^2 value	10	T^2 value
FH x SF	**<0.0001**	0.2783	**<0.0001**	0.8955	**<0.0001**	0.5693	**<0.0001**	4.824
FH x SG	**<0.0001**	0.2807	**<0.0001**	0.8482	**<0.0001**	0.3725	**<0.0001**	1.236
SF x SG	0.9815	0.0073	0.2143	0.0805	0.3254	0.1298	**0.0265**	0.3650

Probabilities in **bold** are significant at the 0.05 level ($P<0.05$).

Table 5.15. Discriminant analysis of flathead chub, sicklefin chub, and sturgeon chub from the study segments.
Discriminating variables were scores on six physiochemical variables for the three cyprinid species.
Relative %=relative contribution to total dispersion.

	Standardized Coefficients for Canonical Variable I	Standardized Coefficients for Canonical Variable II
Segment 5		
Depth (m)	0.4960	-0.1005
Current Velocity (m/s)	0.5631	0.0142
Temperature (Celsius)	0.0306	-0.8184
Turbidity (NTU)	0.0743	-0.0210
%Sand	0.1730	0.5469
%Silt	-0.3034	0.3949
Eigenvalue	0.3644	0.0019
Relative %	99	1
Segment 8		
Depth (m)	-0.6300	0.0546
Current Velocity (m/s)	-0.4956	-0.4263
Temperature (Celsius)	-0.0898	0.2237
Turbidity (NTU)	0.3109	0.1123
%Sand	-0.0745	1.0705
Eigenvalue	1.0253	0.0144
Relative %	99	1
Segment 9		
Depth (m)	0.7737	-0.7
Current Velocity (m/s)	0.0642	1.3555
Temperature (Celsius)	0.0001	0.1261
Turbidity (NTU)	0.0611	-0.3369
%Sand	0.1525	0.2558
%Silt	-0.2838	0.5023
Eigenvalue	0.4897	0.0617
Relative %	89	11
Segment 10		
Depth (m)	-0.4771	-0.4599
Current Velocity (m/s)	-0.6914	0.4691
Temperature (Celsius)	-0.0224	-0.7037
Turbidity (NTU)	0.2315	0.7117
%Sand	-0.3305	-0.3903
%Silt	-0.1837	-0.0759
Eigenvalue	2.8946	0.0810
Relative %	97	3

Table 5.16. Classification matrix derived from discriminant analysis with the percent classified correctly and the percent classified incorrectly for each species in a segment.

		N	% classified correctly	Flathead chub	Sicklefin chub	Sturgeon chub
Segment 5						
	Flathead chub	208	84.1	74.1	10.0	15.9
	Sicklefin chub	68	0.0	49.3	0.0	50.7
	Sturgeon chub	88	50.0	50.0	0.0	50.0
Total			60.1			
Segment 8						
	Flathead chub	134	88.9	88.9	0.0	11.1
	Sicklefin chub	51	7.3	7.1	7.3	85.6
	Sturgeon chub	57	64.9	12.2	22.9	64.9
Total			70.1			
Segment 9						
	Flathead chub	196	76.4	76.4	2.1	21.5
	Sicklefin chub	52	20.9	10.0	20.8	69.2
	Sturgeon chub	145	68.3	26.2	5.5	68.1
Total			63.1			
Segment 10						
	Flathead chub	101	96.0	96.0	0.0	4.0
	Sicklefin chub	42	89.7	0.0	89.7	10.3
	Sturgeon chub	48	36.4	18.2	45.4	36.4
Total			84.1			